MODERN GIRAFFES AND THE FOSSIL GIRAFFIDS OF AFRICA[1]

RONALD SINGER[2]
Anatomy Department, University of Cape Town[3]
and
EDOUARD L. BONÉ
Palaeontology Department, Geological Institute, University of Louvain, Belgium

The publication of this paper was in part made possible by a grant from the 'Fondation Universitaire' of Belgium and the South African Council for Scientific and Industrial Research.

CONTENTS

GENERAL INTRODUCTION

With the discovery of several large fossilized giraffid teeth (Singer, 1954) and, later, of a pair of horn cores (so-called 'palmated antlers') on the large exposed sand-duned fossiliferous site on the farm 'Elandsfontein' near Hopefield (60 miles north-west of Cape Town), it was found necessary to compare these specimens with others found in Africa. During this study, it became obvious that a complete survey and review of the numerous genera of fossil giraffids found on the continent was essential. On surveying the literature, very little information on the extant *Giraffa camelopardalis* was found. Consequently a large number of skeletons of the extant animal were studied in the American Museum of Natural History (New York), in the Chicago Natural History Museum, in the U.S. National Museum (Washington, D.C.), in the Department of Comparative Zoology at Harvard University, in the Musée Royal du Congo Belge (Tervuren, Brussels), and in the South African Museum, Cape Town, so as to obtain statistically significant ranges of variation of intra-specific

[1] Summary read at the 5th INQUA Congress, Barcelona in September, 1957.
[2] Honorary Curator of Human Palaeontology, South African Museum, Cape Town.
[3] Visiting Professor in Anatomy, University of Illinois, Chicago (1959–60).

characters which would be of value in assessing the fossil specimens. This paper is consequently divided into three* portions, the first dealing with observations on the modern giraffes, the second containing observations on the fossil material assembled in Cape Town or studied in the British Museum (Natural History), the Muséum d'Histoire Naturelle (Paris), and the Coryndon Museum, Nairobi, while the third section contains the discussion and conclusions.

SECTION I

SURVEY OF THE LIVING GIRAFFE

Introduction

In the literature numerous references are made to various subspecies of *G. camelopardalis*. These distinctions are based on skin colour pattern and on horn-core differences (Lydekker, 1904). Owing to the fact that the skins of the extant specimens studied were not preserved in most cases, no correlation with the skeletal material was possible, but the study of the horn-cores (*vide infra*) indicated that no substantial subspecific differences could be detected, and consequently it was considered reasonable to treat the material as a whole in a specific determination. As a result of the observations made and the wide range of variation of the data obtained for the whole group, it is suggested that the diagnostic criteria for subspecies of *G. camelopardalis* should not be based on skin colour patterns alone as these may be ecological variables. In this respect, it is interesting to observe in the list of extant specimens examined (Chapter 2) that the deficiencies in the information regarding the subspecies in Museum records are due to the fact that no accurate diagnosis was possible on the basis of the skeleton alone when no skin was received.

CHAPTER I

GENERAL DESCRIPTION OF THE GIRAFFID DENTITION

(Applicable to modern giraffes and extinct giraffids.)

While almost all the Eocene Ungulata possess the full mammalian dentition ($I\frac{3}{3}\ C\frac{1}{1}\ P\frac{4}{4}\ M\frac{3}{3} = 44$), maxillary incisors and canines as well as anterior upper and lower premolars and posterior molars have been lost in the course of the evolution of the Giraffidae, so that all recorded fossil material already possess the formula of the extant giraffes, viz. $I\frac{0}{3}\ C\frac{0}{1}\ P\frac{3}{3}\ M\frac{3}{3} = 32$. The mandibular incisors must have occluded —as in the modern Pecora—against a hard elastic pad of the gum. Parallel to this reduction in the number of teeth, a great development of the cheek-teeth is observed, as well as a marked tendency to hypsodonty (less noticeable in the modern species), both characters making the dental apparatus suitable for a herbivorous diet, which

* A fourth portion, the Appendix, was added later.

requires a great amount of mastication. In the general pattern of the teeth, there is no essential difference between fossil and extant Giraffidae, although quite a few of the fossil genera have got much larger teeth as well as minor variations in structure. As far as it can be judged from the extinct material available, the whole family is characterized by a brachy- to hypsodont, selenolophodont type of molar. In all specimens, the third lower molar has an accessory posterior lobe or talonid. The somewhat cuboid crown of the molars presents on its occlusal surface—even before any marked wear—a longitudinal fold, extending across the summit mesio-distally, and a transverse cleft extending bucco-lingually, dividing the tooth into an anterior and a posterior lobe or pillar. The external surface presents two vertical grooves running from the grinding surface to the root, the buccal one being by far the deepest in the lower molars, the lingual one in the upper; the less marked groove on either surface is actually nothing more than the lateral depression resulting from the formation of a mesostyle by an elevation of the cingulum (*vide infra*). Each of the pillars of the molars are slightly angulated through their transverse axes to the main longitudinal axis of the jaw so that the former axes are rotated anteriorly and medially: the anterior portion or pillar of a particular molar lies more laterally (buccally) than the posterior pillar of the preceding molar.

It is not essential here to present details and discussion about the origin of the Ungulate tooth and its components, but a brief description of the structure of the giraffid tooth is justified for the sake of clarity.

In earlier mammalian forms, trigone and talon distinguish between cutting and crushing portions of the crown, but the trigone is lowered in Ungulates to the level of the talon. Four main primary cusps may be recognized in the molars, while a fifth one, derived from the cingulum, has probably been established very early as a further crown cusp. These five *cones* (or *conids* in the lower molars), which are elevations of the grinding surface of the tooth, eventually become separated from one another by small secondary and intermediate cusps, *conules* or *conulids*. The periphery of the base of the crown, or *cingulum*, encircles the neck of the tooth: it is well or little developed, depending on a rather wide individual variation. Nevertheless it is nearly always present and commonly gives origin to peripheral cusps, called *styles* or *stylids*. In this paper, cusps are named according to the tritubercular theory of Osborn (1892), but this does not necessarily indicate that there is an acceptance of all its broad phylogenetic implications. As this paper is exclusively devoted to Giraffids, the main purpose of utilizing Osborn's nomenclature is to provide a clear description of morphological features. However, in this respect, the suggestions of Arambourg (1947) are very helpful, because his amended nomenclature may be applied both to molars and premolars. Main cusps will therefore be called *cones* or *conids*. The medial (lingual) ones are, in the upper teeth, from front to back (mesio-distal), the *protocone* and the *hypocone*, in the lower teeth the *paraconid*, the *metaconid* and the *entoconid* (fig. 1). The lateral (buccal) cusps are, respectively, the *paracone* and the *metacone*, and the *protoconid* and the *hypoconid*. Secondary cusps in the upper teeth are the intermediate *paraconule* and *metaconule*, derived from elevations of the crown, and, in the lower, the *hypoconulid*. Other secondary cusps are also derived from elevations of the cingulum, viz. the lateral *parastyle*, *mesostyle* and *metastyle*, and the *protostylid*, *ectostylid* and *hypostylid* of upper and lower molars respectively, while on the medial side are the *protostyle*, *entostyle* and *hypostyle*, and the *parastylid*, *metastylid* and *entostylid* on the upper and lower teeth respectively.

In the Ungulate type of tooth, especially among Pecora, several cusps or *styles* lose their individuality and fuse into crests or ridges or *lophs*. These are built up of

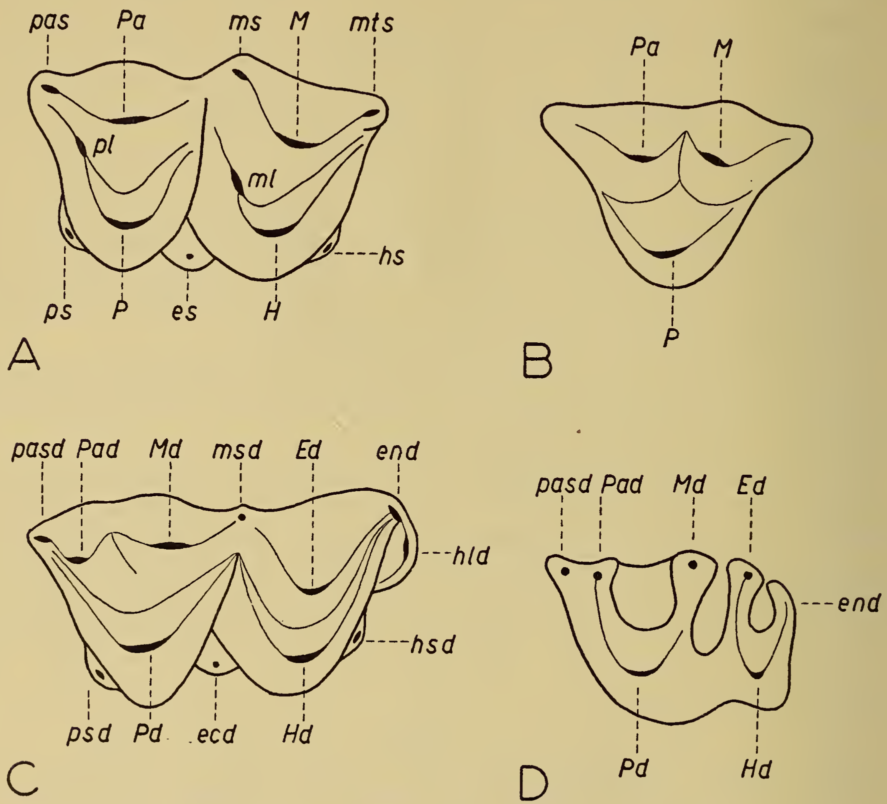

Fig. 1. Schematic representation of giraffid molar and premolar nomenclature (after Arambourg, 1947).
A, upper molar. B, upper premolar. C, lower molar. D, lower premolar.

			Upper jaw		*Lower jaw*	
Main cusps	*Internal*	1.	Protocone	P	Paraconid	Pad
		2.	Hypocone	H	Metaconid	Md
		3.			Entoconid	Ed
	External	1.	Paracone	Pa	Protoconid	Pd
		2.	Metacone	M	Hypoconid	Hd
Secondary cusps	*Median* anterior		Paraconule	Pl		
	posterior		Metaconule	ml	Hypoconulid	hld
	External	1.	parastyle	pas	protostylid	psd
		2.	mesostyle	ms	ectostylid	ecd
		3.	metastyle	mts	hypostylid	hsd
	Internal	1.	protostyle	ps	parastylid	pasd
		2.	entostyle	es	metastylid	msd
		3.	hypostyle	hs	entostylid	end

two or more cusps and are ordinarily very marked, so that *protoconule* and *protocone*, *metaconule* and *hypocone*, *parastyle*, *paracone*, and *mesostyle*, and *mesostyle*, *metacone* and *metastyle* (or corresponding *conids* and *stylids* in the lower tooth) are fused forming four of these crescentic ridges or 'crescents', the former two being more curved, and the concavity of the crescents facing the buccal or lingual surface of the tooth in the upper and lower molar, respectively. This double-pillared and double-crescentic crown is the typical simple ruminant pattern and determines the seleno-lophodont type of Giraffid tooth.

Prolonged into the depth of the crown by their enamel coat, the two parallel rows of cusps and their linking crests [the buccal and the lingual, i.e. the *proto-hypoloph* (*metaloph*, Osborn, 1907) and *ectoloph*] build the side-walls of the *infundibulum*, central pit or valley, poorly lined by cement (*crusta petrosa*) in Giraffids, which becomes stained by the food and constitutes the so-called *mark* (*Marken*, Bohlin, 1926; *marque*, Arambourg, 1947). The *infundibulum* is itself festooned along the mesio-distal axis of each pillar, and is contiguous in the transverse cleft with the central pit of the adjacent pillar before any advanced wear takes place. When unworn, the crescentic ridges are very well marked. With the gradual wear of the pointed enamel crests, however, the apex of each *loph* tends to be levelled mesio-distally while the *lophs* broaden in the bucco-lingual axis. An increasing crescentic tract of dentine shows between the two newly formed lips of enamel which progressively separate from one another; at that time the *infundibulum* or central pit narrows by approximation of the buccal and lingual lips of the adjacent walls of the crescents. In very worn teeth, the pit may be restricted to a simple ridge of enamel, circular (island of enamel) or linear, which represents the actual fusion line of the side walls of the *infundibulum* in the depth of the crown, or the enamel of the pit may even disappear completely.

It has often been observed and mentioned (already by Owen, 1840–5) that in the giraffe, the median convexity (*costa*) of the buccal surface of the anterior pillar in upper teeth (inner or lingual surface, in lower teeth) is more prominent nearer the occlusal end of the crown than nearer the base, while the vertical ridge of the *meso-style* (*-stylid*) projects outwards from the surface of the tooth more than the median *costa* of the *metacone* (or *entoconid*). This feature is quite consistent throughout the family, and is distinctly recognized in the fossil material from the Siwaliks, India, as well as in the specimens presently studied (*vide infra*).

The upper molars differ from the lower molars in their general shape, the breadth or transverse (bucco-lingual) diameter approximating or even surpassing the length or antero-posterior (mesio-distal) measurement.

As in most artiodactyls, the premolars are unilobed. However, in the fossil specimens the last lower premolar has a clear demarcation of the posterior portion of the tooth.

The incisors describe a semicircle, although in most ruminants they are arranged in a straight transverse line at the extremity of the jaw. The canines have been profoundly modified in shape and position and resemble very much a fourth pair of incisors; however their crown is larger, much more triangular and somewhat bilobed.

All the teeth are covered by a coat of relatively very rugose enamel, both on the extant and fossil specimens. This feature is characteristic of the group. The maximum rugosity is always observed on the medial surface of the *protocone* and *hypocone*, and on the lateral surface of the *protoconid* and *hypoconid.*

Incisors and canines are implanted by a single root which slopes backwards horizontally. The lower teeth have two roots, an anterior and a posterior one; all the upper teeth have three roots, two lateral and one medial. However, both anterior and posterior roots of the lower molars as well as the medial root of the upper molars show a tendency of fusion of two fangs. They are broadened, flattened from side-to-side or bucco-lingually, and present a median groove, the groove being on the lingual surface in the upper, while in the lower the groove on one root faces that on the other, the deeper groove being on the anterior root.

CHAPTER 2

LIST OF RECENT *GIRAFFA CAMELOPARDALIS* STUDIED

The observations recorded below on the extant material were made on the following specimens, for which the number, age, sex, origin and subspecies have been extracted directly from the registers of the respective museums. Gaps in the information below indicate deficiencies in the registers.

I. U.S. NATIONAL MUSEUM, WASHINGTON, D.C.

No.	*Subspecies*	*Age*	*Sex*	*Origin*
14411	*G.c. camelopardalis*	I[1]	—	—
121010	*G.c. rothschildi*	A[1]	M	Lake Baringo, B.E.A.[2]
154033	*G.c. capensis*	I	M	Matabeleland, Rhodesia.
155438	*G.c. rothschildi*	A	M	Guas Ngishu Plains, B.E.A.
162016	*G.c. tippelskirchi*	A	—	Kilima Kui Kapiti Plains, B.E.A.
162017	*G.c. tippelskirchi*	A	M	Kilima Kui Kapiti Plains, B.E.A.
162018	*G.c. tippelskirchi*	A	M	Ulu Station, B.E.A.
162988	*G.c. tippelskirchi*	A	F	Sotik, Gnaso Nyiro, B.E.A.
162989	*G.c. tippelskirchi*	I	F	Sotik, Gnaso Nyiro, B.E.A.
163112	*G.c. rothschildi*[3]	I	M	Guas Ngishu Plateau, B.E.A.
	G.c. tippelskirchi	I	M	Sotik, Gnaso Nyiro, B.E.A.
163113	*G.c. reticulata*	A	—	Gnaso Nyiro, B.E.A.
163312	*G.c. rothschildi*	A	—	Guas Ngishu Plateau, B.E.A.
163324	*G.c. reticulata*	A	F	N. Gnaso Nyiro, B.E.A.
182124	*G.c. reticulata*	A	—	Koga Water, B.E.A.
182125	*G.c. reticulata*	A	—	Marsabit Road, B.E.A.
182192	*G.c. reticulata*	A	—	Lakiundu River, B.E.A.
200151	*G.c. rothschildi*	A	M	Wasin Gisher Plateau, B.E.A.
251797	*G.c. tippelskirchi*	A	F	Savanda, Dodoma, Tanganyika.
251798	*G.c. tippelskirchi*	A	—	Dodoma, Tanganyika.
251799	*G.c. tippelskirchi*	A	—	Mkata Plains, Tanganyika.
251800	—	A	—	—
252549	—	I	M	Sudan (Nat. Zool. Park).
252585	—	I	F	Sudan (Nat. Zool. Park).
270594	*G.c. reticulata*	A	F	— (Nat. Zool. Park).
279405	—	9 years	M	— (Nat. Zool. Park).
296145	—	A	—	S.W.A.[2], Gaucha (about 19° 47′ S. 20° 35′ E.).
299998	*G.c. camelopardalis*	I 5 months 26 days	M	— (Nat. Zool. Park).

II. CHICAGO NATURAL HISTORY MUSEUM

No.	*Subspecies*	*Age*	*Sex*	*Origin*
27475	—	I	M	Northern Uganda.
29515	—	I	F	Kenya.
32901	*G.c. reticulata*	A	F	Abyssinia, Sidamo, Boram Border.
32902	—	A	F	Abyssinia, Sidamo, Boram Border.
32904	*G.c. reticulata*	I	M	Abyssinia, Sidamo, Boram Border.
32905	—	I	M	Abyssinia, Sidamo, Boram Border.
34422	—	A	M	Bechuanaland, Mababe Flats.
34423	—	A	F	Bechuanaland, Mababe Flats.
34424	—	A	F	Bechuanaland, Mababe Flats.
34425	—	A	M	Bechuanaland, Kalahari Desert, Kwaai, Mokaba River.
34426	—	A	F	Bechuanaland, Mababe Flats.
34427	—	I	F	Bechuanaland, Mababe Flats.
34428	—	I	M	Bechuanaland, Mababe Flats.
34429	—	A	F	Bechuanaland, Mababe Flats.
34930	—	A	M	Kenya.
53765	*G.c. reticulata*	A	M	—
54251	—	I	M	Tanganyika (Zoo).
X_3 (4)	—	A	—	—

III. COMPARATIVE ZOOLOGY MUSEUM, HARVARD UNIVERSITY

8370	*G.c. tippelskirchi*	A	—	East Africa.
8371 (5)	—	A	—	—
8372 (5)	—	A	—	—
14564	*G.c. tippelskirchi*	A	—	B.E.A.
15698	—	A	—	Sudan, Dinder River, near Kuka-Dindu.
27137	—	A	—	East Africa.

IV. AMERICAN MUSEUM OF NATURAL HISTORY, NEW YORK

20884	—	I	F	—
24290	—	A	—	Bechuanaland.
24291	—	A	—	Bechuanaland.
24292	—	A	—	Bechuanaland.
24293	—	A	—	Bechuanaland.
27675	—	A	—	Kenya.
27752	*G.c. rothschildi*	A	—	B.E.A.
27753	*G.c. rothschildi*	I	—	B.E.A.
35536	—	A	M	—
35628	—	I	—	—
53543	*G.c. congoensis*	A	F	Belgian Congo.
53544	*G.c. congoensis*	I (Foetus)	—	Belgian Congo.
53546	*G.c. congoensis*	A	F	Belgian Congo.
53548	*G.c. congoensis*	I	M	Belgian Congo.
53549	*G.c. congoensis*	A	F	Belgian Congo.
54122	*G.c. tippelskirchi*	I	M	B.E.A.
54123	*G.c. tippelskirchi*	A	M	Northern Gnaso, Nyiro.
57675	—	A	—	—
69403	—	I	—	—
80146[1] (6)	—	I 7 months	M	(New York Zoo)
80146[2] (6)	—	I	—	—
81820	—	A	—	—
81821	—	A	—	—
81822	—	A	—	—
81823	—	A	—	—
81824	—	A	—	—
81825	—	I	—	—
81826	—	I	—	—

No.	*Subspecies*	*Age*	*Sex*	*Origin*
82001	—	A	M	Kenya.
82002	—	A	F	Kenya.
82003	—	I	—	Kenya.
83458	—	I	F	Bechuanaland, Mababe Flats.
83459	—	I	F	Bechuanaland, Mababe Flats.
83460	—	A	M	Bechuanaland, Mababe Flats.
83605	—	I	—	Southern Rhodesia, east of Ngamo Station.
99493	—	A	M	Nubia (23 years in a zoo).
139695	—	A	—	—
139696	—	A	—	—
144915	—	A	—	(Central Park Zoo, N.Y.).
165051	*G.c. capensis*	I	M	S.W.A., Etosha Pan, Farm Lombard.
165052	*G.c. capensis*	I	F	S.W.A., Etosha Pan, Farm Lombard.
X_1 (7)	—	A	—	—
X_2 (7)	—	A	—	—
X_4 (7)	—	A	—	—
	V. SOUTH AFRICAN MUSEUM, CAPE TOWN			
M. 245	—	I	—	—
17176	—	A	—	—
—	—	A	—	—
	VI. MUSÉE ROYAL DU CONGO BELGE (TERVUREN, BRUSSELS)			
R.G. 4947	*G.c. congoensis*	A	—	Uele.
R.G. 4948	*G.c. congoensis*	A	—	Uele.
R.G. 4949	*G.c. congoensis*	A	M	N.E. Uele; sources of Garamba River.
R.G. 6342	*G.*	A	—	Ufipa district.
R.G. 2128	*G.c. schilbergsi*	A	—	B.E.A., Serengeti Plains.

(1) 'I' signifies immature; 'A' = adult.

(2) B.E.A. signifies British East Africa; S.W.A. = South West Africa.

(3) The same number has been given to the skull and the jaws. Although they obviously belong to the same individual, the skull is labelled '*rothschildi*' and the jaws '*tippelskirchi*', and they have been given different places of origin.

(4) This specimen has no Collection number. This indication is ours.

(5) Although skull and jaws have the same number they do not belong to the same individual.

(6) These two specimens have the same number. We refer to them as (1) and (2).

(7) These three specimens are not registered. We refer to them as X_1, X_2 and X_4.

CHAPTER 3

OBSERVATIONS ON TOOTH ERUPTION AND CRANIAL SUTURES

Among the specimens examined, a group of 32 immature individuals forms a rather complete series of the various juvenile and adolescent stages of growth. In describing this series, the sequence of tooth eruption and cranial suture synostosis, and some data concerning the milk dentition and the growth pattern are particularly emphasized.

From the information available, it is possible to extract the subspecies of *Giraffa camelopardalis* in 12 cases: *camelopardalis* (2), *rothschildi* (2)*, *tippelskirchi* (2), *congoensis*

* The same number (U.S. Nat. Mus. 163112) has been given to the skull and the jaws. See note (3) in legend in previous chapter.

(2), *reticulata* (1) and *capensis* (3). As far as the sex is concerned, 10 specimens were registered as female, 13 others as male. As regards their origin, it is known that 8 animals derive from British East Africa, 2 from Sudan, 2 from Ethiopia (Abyssinia), 2 from the Belgian Congo, 2 from Southern Rhodesia, 4 from Bechuanaland and 2 from South West Africa. Some specimens of unknown origin had been received from zoological gardens or veterinary colleges. The ages extend from the foetal period to the sub-adult stage. Information concerning the precise age of two specimens were found in the Museum registers, viz., specimens 299998 and 80146[1] which are 5 months 26 days and 7 months old respectively; unfortunately the latter animals were born, reared and then died in zoos. It is quite likely that conditions of captivity affected the growth tempo, and data concerning these must be evaluated with care before using them as age standards.

A. Tooth eruption

In the group of immature animals 826 teeth were available for study (table 1). In this number are also included the sockets of missing teeth. Furthermore, although

Permanent Dentition (411)	I_1	I_2	I_3	C	P^2	P_2	P^3	P_3	P^4	P_4	M^1	M_1	M^2	M_2	M^3	M_3
	22	16	12	6	18	14	19	18	18	18	58	54	44	42	26	26

Milk Dentition (415)	i_1	i_2	i_3	c	DM^2	DM_2	DM^3	DM_3	DM^4	DM_4
	32	36	44	48	42	42	42	42	45	42

Table 1. Number of teeth examined in the immature giraffes.

some of the teeth were either broken or incompletely erupted, valuable information was gained from observations on either their roots or their sockets. Accurate measurements could be made on 331 perfectly preserved milk teeth. The stage of eruption of the dentitions is indicated in table 2 and figure 2.

Erupting Tooth	Stage 1	Stage 2	Stage 3	Stage 4	Absolute Age
DM3	53544				Foetus
M1	163112 34428		299998 82003 80146[2] 83459	14411	6 months
M2		252549 252585 80146[1] 54251		162989 53548 54122 81826	7 months
M3—I1	165052 20884	29515	83605	81825	
P4, P3, P2	35628 27753			69403	
I3	154033 165051			34427	
C	27475 83458			32905	

Table 2. Stage of eruption of individual teeth. The appearance of the tooth at the surface of the bony alveolus is stage 1, while stage 4 indicates complete eruption of the crown. Stages 2 and 3 are equally spaced intermediate phases.

The observations on the state of eruption and wear lead to the following conclusions:

1. For both the milk and permanent dentitions (with the exception of DM^4, *vide infra*), the upper teeth erupt slightly before the corresponding lower teeth. The priority of eruption of a particular upper tooth was observed in 16 of the 18 cases (from 13 different individuals) where the difference between the time of eruption of a tooth in the upper and of a corresponding time in the lower jaw (here called 'asynchronism') could be traced, namely, for M1—80146[2], 82003, 83459; for M2—81826, 53548 and 54251; for M3—81825, 83605, 165052 and 29515; for P2—27753 and 35628; for P3—27753, 35628 and 83605; and for P4—30628. In only two cases the lower tooth has erupted shortly before the corresponding upper tooth, viz. in 69403 (P_2) and 299998 (M_1). In no case, however, is the asynchronism too marked: in the above 18 cases, the more precocious tooth is never fully developed before the lower one starts erupting. Four degrees of actual eruption are defined from the first appearance of the tooth on the alveolar surface (stage 1) to its final development (stage 4); two intermediate stages (stages 2 and 3) of progressive eruption are interposed. The state of development prior to any eruption is termed stage 0. In 17 of the 18 cases the degree of asynchronism does not exceed one unit (i.e. 0—1, 1—2, 2—3, 3—4), while in only one case, viz. the P3 of 35628, is the difference between the stage of eruption of the upper and the lower tooth 2 units (1—3). It is not easy to evaluate the absolute duration (in terms of days, weeks, etc.) of the asynchronism. Eruption may be a rather rapid process because in one particular case (35628), the milk molar DM^4 is still fixed on the summit of a fully erupted P^4. No conclusions can be drawn whether there is lack of asynchronism of eruption between right and left corresponding teeth in a maxilla or mandible. The evidence suggests that they erupt synchronously (fig. 2).

2. The complete milk dentition is *in situ* and is already functional before the first permanent tooth (M^1) erupts, e.g. 80146[2], 82003, 83459, 163112, 299998, 14411 and 34428. The first two incisors i_1 and i_2 probably precede the appearance of the first milk molar. Only one specimen of the collection (53544) is at such an early stage, but because it is rather badly preserved it is not possible to draw a definite conclusion. The first two incisors are perfectly formed and fully erupted before DM_4 begins to come through, but the evidence is not sufficient to ascertain the relationships of i_3 and the canine, although specimen 32904 suggests that the latter appears immediately after all the milk molars have erupted.

3. The milk molars erupt in rather regular succession, posterior to anterior in the mandible, DM_4 preceding DM_3, which in turn precedes DM_2, as in specimen 80146[2] and 53544. Furthermore, the latter is still a foetus and indicates that the whole milk dentition is formed before parturition. The succession is reversed for the maxilla, as judged from specimen 80146[2] where the eruption starts with DM^2. On the other hand the six upper and lower milk molars seem to erupt simultaneously in specimen 32904, so that one cannot generalize dogmatically on the basis of this small series.

4. The permanent molars of both upper and lower jaws erupt in the same order, i.e. from anterior to posterior: M1 precedes M2 in 14 cases (53548, 80146[1], 80146[2], 81826, 82003, 83459, 14411, 163112, 252549, 252585, 299998, 162989, 34428

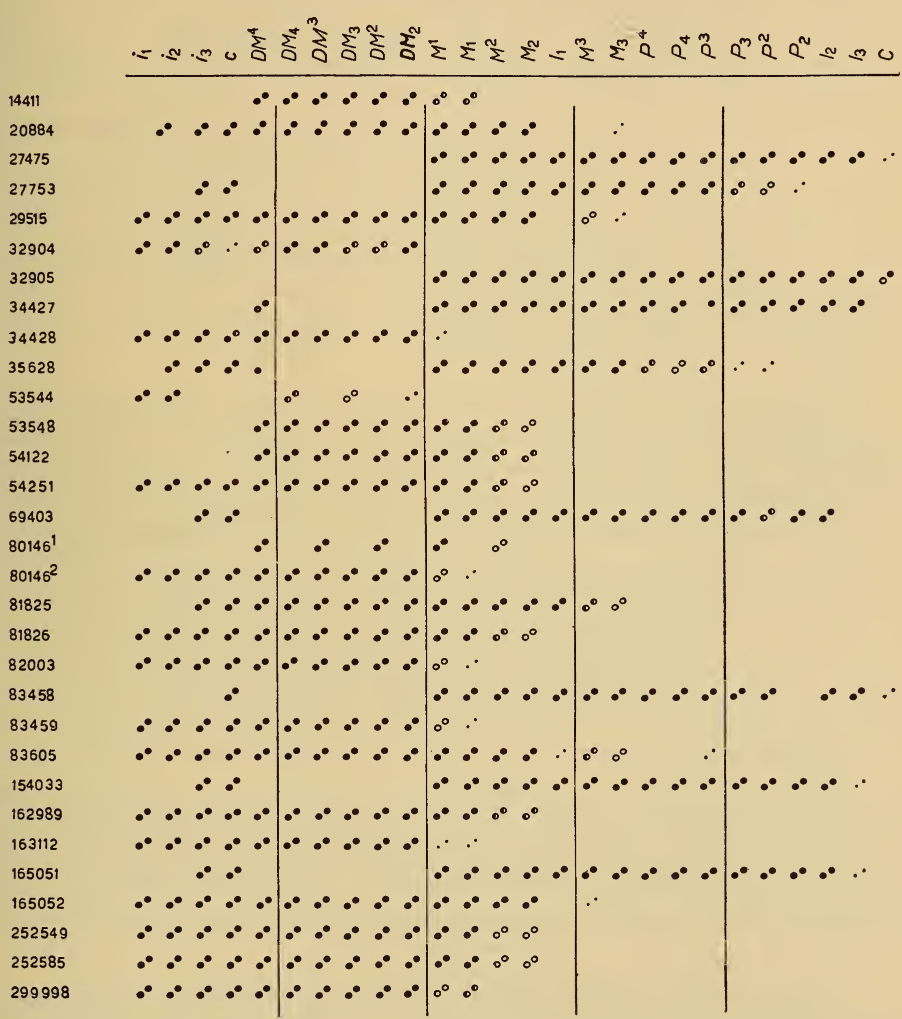

FIG. 2. Stages of eruption of individual modern giraffe dentitions (upper and lower, left and right sides).
. — Stage 1. ○ — Stage 2. ◐ — Stage 3. ● — Stage 4.

and 54251), and M2 precedes M3 in 13 individuals (20884, 53548, 54122, 80146[1], 81825, 81826, 83605, 165052, 252549, 252585, 162989, 54251 and 29515). No exception to this order was found.

5. The replacement teeth of the milk molars, the premolars, usually appear

immediately after the eruption of the last permanent molar, i.e. M3, and never before it. In one case, however, M3 (83605) is still in the process of eruption (stage 3) when P3, the first actual premolar to erupt, already cuts through the alveolar border. The sequence of appearance of the premolars is less rigid than the eruption order of the molars. In the four cases where the observation was possible (25628, 69403, 27753 and 165051), P2 is later than P3; in a fifth case (83458) P2 is bilaterally absent in the mandible, and this might be considered as an extreme of the normal late eruption of P2. In quite a few adult specimens, the same congenital absence of P2 was observed (e.g. 83460, lower left), or alternatively, there is a marked reduction of P2 where the root is abnormal (single) and the body slightly shorter (A—P) than usual (83460, 34423 and 34424). While P4 precedes P3 in two cases (27753 and 35628), P3 erupts before P4 in one specimen (83605). Consequently, it may be concluded that the premolar eruption sequence is variable, but that the whole process of eruption must be rather brief. These small individual differences have probably no or little functional influence or significance.

6. The permanent incisors erupt at the same time as the molars and premolars. In this respect, useful information is provided by 13 mandibles. I_1 starts erupting during the eruption and maturation of M_3 (83605), and it is always present when M_3 has completed its growth (27753, 35628, 69403, 81825, 83458, 83605 and 165051). It might erupt slightly before M_3 (81825); usually, however, it does so immediately after (83605 and 165052). I_2 appears later and never erupts before I_1 or before the full development of all the molars and premolars (27753 and 35628); in both cases, for example, the milk incisor i_2 is still *in situ* when the last erupting premolar (P_2) comes through. On the other hand, specimen 69403 has a perfectly developed I_2 while P_2 is still erupting, which would suggest that both teeth erupt practically simultaneously, unless one considers it as an abnormal delay in P_2 eruption (it being the only recorded case where the upper tooth is slower than the corresponding lower one, and P_2 is in fact perfectly and completely developed). I_3 can be found, though still in eruption, on three specimens (83458, 154053 and 165051) which already have their two other incisors and all their molars and premolars. I_3 is still lacking in four other individuals which have all their premolars (27753, 35628, 69403 and 83605). Consequently, it indicates that the eruption of the lateral incisor I_3 occurs after that of all the other permanent teeth, except the canine.

7. The permanent canine was found in only three specimens of the immature collection (83458, 32905 and 27475). In one of these, it erupts directly under the milk canine which is still *in situ*, all the other permanent teeth being perfectly developed. This animal died during the transition from a sub-adult to an adult stage as is indicated by the fact that the canine is the last tooth to complete the dentition of the giraffe.

Figure 3 illustrates a schematic and summarized view of the above information as well as an attempt to determine the absolute age of tooth eruption in modern giraffes (data completing and correcting Owen, 1840–5, and 1849, as well as Lankaster, 1907).

B. Cranial suture and tooth eruption

In the same group of immature giraffes observations were made on eight sutures: fronto-sagittal, fronto-parietal, inter-parietal, temporo-parietal, temporo-occipital,

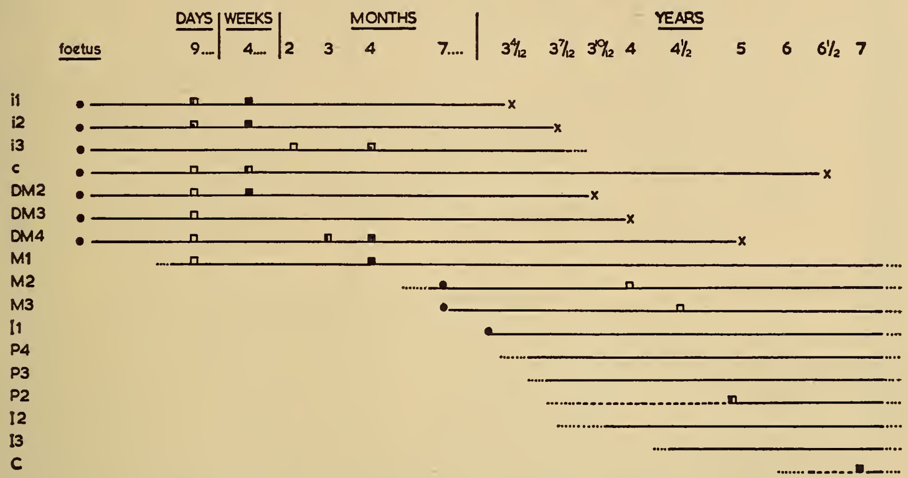

Fig. 3. Schematization of the order of eruption of teeth in *Giraffa camelopardalis* and a determination of the absolute age of tooth eruption.

● — Teeth deeply embedded in bony alveolus (Stage 0).
□ — Begins to erupt through bony alveolar margin (Stage 1).
◰ — Just penetrating through bony margin (Stage 2).
◧ — Crown projecting beyond bony margin (Stage 3).
■ — Crown entirely erupted (Stage 4).
× — Tooth fallen out.

parieto-occipital, exoccipital-supra-occipital and palatal. Three different degrees of synostosis were determined: the bones may be in contact without any trace of closure (0), the suture may be half (1) or completely (2) closed (table 3); see p. 388.

The main conclusions of these observations and of their correlation with the tooth eruption order (fig. 4) are:

1. The inter-parietal suture closes first, rather early, probably at the time of eruption of M1, and is immediately followed by the closing of the parieto-occipital suture. The examination of these sutures was possible in only 20 specimens, but in only one case (83459) the parieto-occipital suture had not started to close, although M1 was already erupting (stage 3) and the closure of the inter-parietal suture was slightly delayed (half-closed), but this may be an individual variation and does not affect the general observations.

2. The occipital suture is the next to be fused. It is always closed when P3 erupts; in fact there seems to be a definite tendency to fuse even earlier, namely, during the eruption of the molars, as seen in 34428, 80146[1], 20884, 29515 and 83605.

Specimen	*Fronto-Sagittal*	*Fronto-Parietal*	*Inter-Parietal*	*Parieto-Temporal*	*Parieto-Occipital*	*Temporo-Occipital*	*Exoccipital-Supra-Occipital*	*Palatal*
32904	0	0	0	0	0	0	0	0
53544	0	0	0	0	0	0	0	0
34428	2	2	2	2	2	0	2	0
82003	0	0	2	0	1	0	0	0
83459	0	0	1	0	0	0	0	0
80146[1]	0	0	2	0	2	0	2	0
54251	0	0	2	0	2	0	0	0
54122	0	0	2	0	2	0	0	0
81826	0	0	2	0	1	0	0	0
165052	1	0	2	0	2	0	0	0
20884	0	0	2	1	2	0	1	0
29515	?	0	2	0	2	0	2	0
83605	0	0	2	0	2	0	1	0
81825	0	0	2	0	2	0	0	0
35628	1	2	2	1	2	0	2	0
27753	1	0	2	1	2	0	2	1
69403	0	0	2	0	2	0	2	0
165051	2	0	2	0	2	0	2	0
34427	2	0	2	0	2	0	2	0
27475	2	0	2	0	2	0	2	0
83458	1	1	2	0	2	0	2	0
32905	2	2	2	0	2	0	2	0

TABLE 3. Cranial suture closure in immature giraffes. The skulls have been graded according to their dental age (see text, and fig. 4 where the same information on the degree of suture closure is correlated with the tooth eruption order).

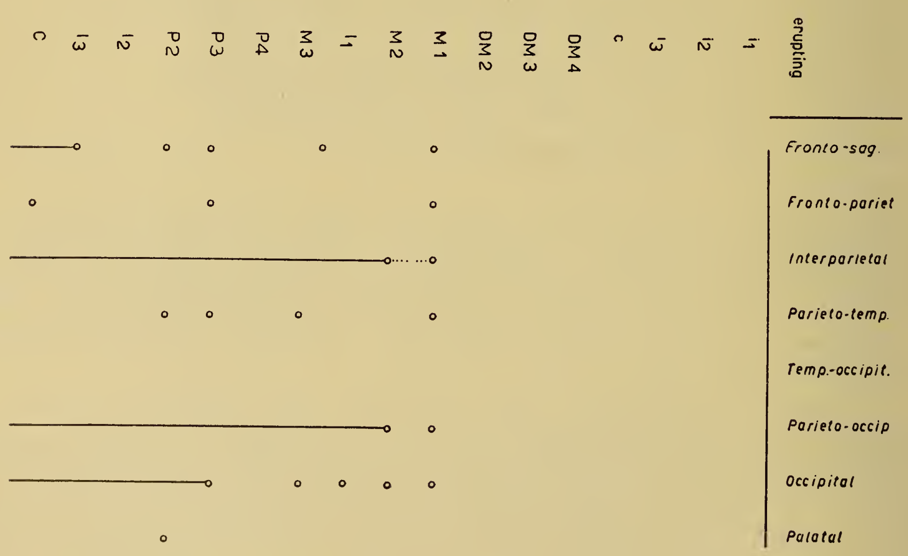

FIG. 4. The relationships between cranial suture closure and tooth eruption order in *Giraffa camelopardalis*.

O : Suture fused, at least at age of the tooth eruption stage.

—O : From the stage of eruption of this tooth onwards, all specimens found with the suture fused, i.e. in one specimen the occipital suture fused at age of eruption of M1, in another at age of eruption of M2, etc. . . .

3. The fronto-sagittal suture is always completely fused when the lateral incisor erupts, although again there is a tendency to fuse earlier (at the time of eruption of M3 or of the premolars).

4. The fronto-parietal suture fuses at the end of the sub-adult period of growth, but, as a general rule, it is not completely fused before completion of growth.

5. The temporo-occipital and the palatal sutures close much later, during adult life, although the latter has been observed partially fused in one case (27753) at the eruption of P2. It has already been mentioned that late synostosis or retardation of closure may occur as an individual variation, and similarly, an acceleration has been observed in specimen 34428, in which, at the time of eruption of M1 (stage 1), all the sutures normally fusing during juvenile or sub-adult life are already completely closed.

C. Skull growth and cranial measurements

From a few cranial measurements (table 4), it is possible to draw some conclusions about growth patterns in modern giraffes. First of all, the ratio fronto-sagittal length/basion-nasal length is practically constant, the range of variation being relatively very small (31·6–36·9) and not altering with the growth gradient. Similarly, the ratio basion-palatal length/palato-nasal length is practically constant, indicating that both elements of the skull length (cerebral and facial) grow at a rather parallel tempo.

Specimens from American Museum of Natural History	*Biorbital diameter*	*Basion-palatal*	*Palatal-nasal*	*Maxillary breadth opposite* M^1	*Frontal length*
53544	111				78
82003	178	139	162	104	111
80146[1]	175			112	
83549	180	138	210	106	117
80146[2]	189		163	124	124
53548	217	183	260	127	149
54122	203			129	139
20884	183	165	262	119	143
165052	243	183	297	140	156
81825	251	208	311	145	171
83605	235	194	304	139	171
35628	215	180	305	118	169
27753	255	200	249?	138	176
81826	209	169		133	154
165051	276	219	366	152	191
83458	268	209		142	174
69403	276	207	336	152	177
Specimens from U.S. National Museum					
163112	186	133	208	107	120
14411	162	128	191	106	117
252549	173	146	231	111	121
252585	184	142	203	111	124
299998	177	147	203	113	123
162989	226	170	268	130	143
154033	268	570 (basion-palatal and palatal-nasal together)		149	211

Table 4. Cranial measurements (mm.) of immature modern giraffes. (Basion-nasion distance obtained by addition of basion-palatal and palatal-nasal measurements.)

Comparing further the growth of the fronto-sagittal length and of the biorbital breadth respectively, one sees that parallel to the increasing length of the skull, there is a very slight reduction of the biorbital breadth, and a more marked relative decrease of the maxillary breadth (fig. 5). Another expression of the same trend is that with the increasing absolute biorbital breadth, there is a decrease in the ratio maxillary/biorbital breadth. Thus during the juvenile and adolescent growth periods of giraffes, the upper portions of the skull, both facial and cerebral, develop at a quicker tempo than the lower part of the face, the breadth of which decreases relative to the biorbital breadth and the frontal length.

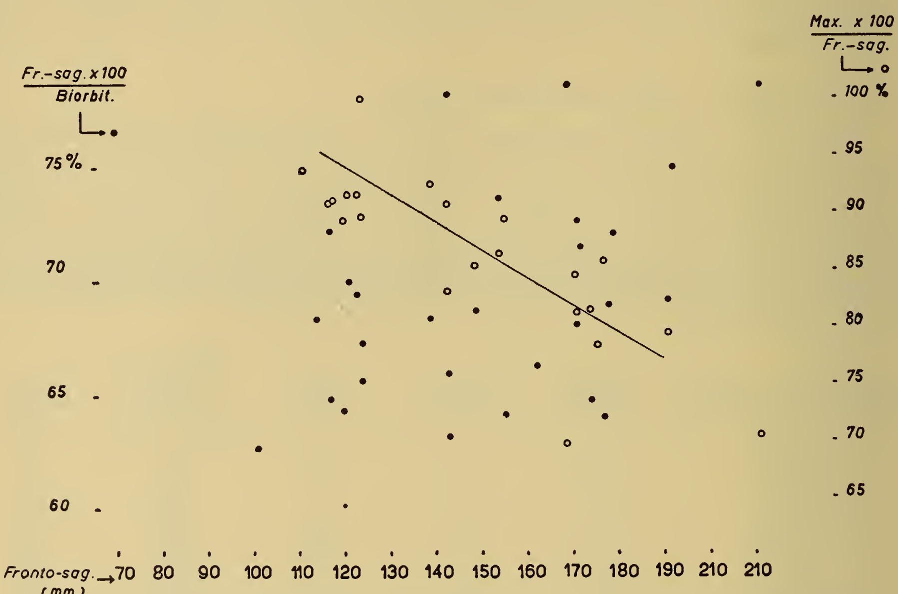

FIG. 5. Comparison of growth of the fronto-sagittal length and of the biorbital breadth.

CHAPTER 4

VARIATIONS OF THE CUSPS OF THE TOOTH CROWN

The variations of cusp-development have been studied in the dentition of the extant giraffe. A large number of teeth have been surveyed (table 5). As regards the cusp-pattern, there is very little difference between right and left corresponding teeth in the same jaw: therefore the observations summarized here will concern only one of each pair of teeth. In the following table, the numbers in brackets indicate the actual number of individual pairs of teeth, while the non-bracketed numbers indicate the actual number of teeth available.

	P2	P3	P4	M1	M2	M3
UPPER	117	120	116	138	130	121
	(59)	(60)	(58)	(69)	(65)	(61)
LOWER	109	124	127	143	135	124
	(55)	(62)	(64)	(72)	(68)	(61)

TABLE 5.

First, the development of the main (crown-) cusps, *cones* or *conids*, and secondly that of the secondary cusps, lateral *styles* or *stylids*, are dealt with. In each section, the molars will be described first, and then the premolars.

MAIN CUSPS

1. Molars. The four main *cones* and the five *conids* of all the molars surveyed show no significant variability. In the upper molars, there is a rather equal development of *proto-* and *hypocone* on the lingual side, while on the buccal aspect, the *paracone* is regularly, and probably typically, more developed than the *metacone* of the same tooth. This is applicable to all true molars, although the vertical *costa* of the *paracone* seems to be more strongly built in M^2 than in M^3, and still more in M^1 than in M^2.

In the lower molars, the fused *para-metaconid* on the lingual surface of the anterior pillar is slightly more developed than the corresponding *entoconid* on the posterior pillar, but the difference does not show as markedly as in the opposing upper tooth. The *talonid* is always very well defined in M_3: its A–P occlusal length, measured in 78 cases, is 23·3% ($\pm$ ·31) of the total mesio-distal length of the tooth (range of variation: 16·5–30·8; $\sigma = 2{\cdot}70$).

2. Premolars. The premolars show the typical main cone pattern: the unilobed upper premolars have three cusps—the *protocone* is on the lingual side, and the *paracone* and *metacone* on the buccal side are fused into one single enamel crest which terminates mesio-buccally in the *parastyle*. In the lower premolars the more complicated but typical features of the giraffid tooth are always recognizable: *paraconid* and *metaconid* are fused into one single mesio-lingual ridge on P_4, but they are more isolated on the anterior premolars when the *paraconid* is much smaller, while in P_2 it is restricted to an ill-defined formation on the outer (buccal) border of the crown. The *entoconid* is always very well defined and linked with the *protoconid* on the buccal aspect by means of a strong ridge of enamel running outwards (buccally) and forwards (mesially) across the horizontal surface of the tooth The *hypoconid* on the buccal aspect is always markedly separated from the *protoconid* by a well-defined vertical furrow which, however, decreases from the grinding surface downwards and disappears before reaching the bulging of the crown well above the margin of the crown-root junction

SECONDARY CUSPS

The observations indicate that there is little variation in the main cusp pattern of the modern giraffe teeth. In contrast, the secondary cusps show a marked degree of individual variation, some of the most characteristic expressions of which will be described below. No emphasis will be placed on the median anterior or posterior cusps, *para-* and *metaconule* respectively, because it is almost impossible to distinguish these formations in many cases, as the demarcation between them and the *proto-* or *hypocone* is hardly noticeable along the *proto* or the *hypo-* (*meta-*) *loph*.

Vertical elevation of the cingulum to form *styles* or *stylids* on the peripheral enamel coat of the tooth is common. Various features can be observed which, for the sake of clarity, are classified here into two main types: (*a*) the *ridge*-type and (*b*) the *column*-type. Variations of both types are quite numerous.

(*a*) the thin *ridge* of enamel may appear either as a straight or a notched crest, and may even have a comb-like appearance distally detached from the crown (fig. 6).

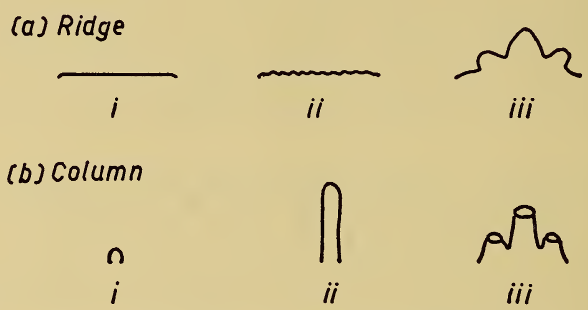

Fig. 6. Types of styles or stylids developing from the cingulum in *Giraffa camelopardalis*.

(*b*) The *column* type presents as a better defined formation rising from the cingulum or the enamel coat either as a small tubercle or a developed narrow column or pillar. In some cases this column appears to be truncated and flanked on both sides by smaller tuberosities.

The column type secondary cusps are always found on molars and premolars, anterior and posterior to the buccal *paracone* and *metacone*, and to the lingual *para-metaconid* and *entoconid* of upper and lower teeth respectively, i.e. *parastyle* and *-stylid**, *mesostyle* and *metastylid*, *metastyle* and *entostylid*. The *parastyle* and *metastyle* in the upper premolars, the *parastyle* and *mesostyle* in the upper molars, the *entostylid* in the lower premolars, and the *metastylid* and the *entostylid* in the lower molars are typically the best defined and the least variable of these lateral (buccal upper or lingual lower) secondary cusps.

On the other hand, the lingual surface of the upper teeth and the buccal and posterior surfaces of the lower teeth show a very marked variation in their *styles*

* The column-like *parastylid* however is usually rather poorly developed. In a few cases, it was even observed being replaced by a more ill-defined crest-like *stylid*. This latter feature is shown in one P_3, two P_4, two M_1, five M_2 and five M_3.

(*stylids*). Indeed, in this region, both types of cusps occur, but it should be noted that while the ridge-type has been observed on both premolars and molars, the column-type has only been observed on molars. Furthermore, while ridges may represent the *protostyle* (*-stylid*), the *entostyle* (*-stylid*), the *hypostyle*, the *ectostylid* or the *hypoconulid*, the column type secondary cusps recorded are ALL (on these surfaces) *entostyles* (*-stylids*) and *ectostylids*. Such formations on the lingual surface of the upper teeth and on the buccal and posterior surfaces of the lower teeth have been observed in 294 cases of the 754 pairs of teeth studied; in six cases, however, two *styles* were observed on the same tooth, so that the actual proportion of teeth affected by these secondary *styles* (*stylids*) is 38·2%. The following table illustrates the distribution of these *styles* among the types of teeth; the figures in italics represent the column-type *styles*, while the non-italicized ones represent the ridge-type cusps.

	P2	P3	P4	M1	M2	M3
Protostyle	1 (1·7%)	1 (1·7%)	1 (1·7%)	5 (7·2%)	5 (7·7%)	4 (6·5%)
Entostyle	7 (11·9%)	7 (11·7%)	6 (10·3%)	1 (1·4%)		
				27 (39·2%)	*25* (38·4%)	*33* (54·1%)
Hypostyle	4 (6·8%)	5 (8·3%)	5 (8·6%)			1 (1·6%)
Protostylid	2 (3·6%)	4 (6·5%)	2 (3·1%)	20 (27·8%)	18 (26·5%)	17 (27·9%)
Ectostylid		1 (1·6%)		1 (1·4%)	2 (2·9%)	2 (3·3%)
				43 (59·7%)	*20* (29·4%)	*18* (29·5%)
Hypoconulid		1 (1·6%)	1 (1·6%)	1 (1·4%)	1 (1·4%)	1 (1·6%)
Entostylid						2 (3·3%)

Table 6. Distribution of secondary cusps in extant giraffe teeth. (Bracketed figures indicate percentage of pairs of teeth available.)

The above figures show clearly the degree of variation of secondary cusp formation in the extant giraffe dentition. It indicates that the tendency for such additional features is much more developed in the molars than in the premolars, and it is probably more in the lower than in the upper teeth. In the upper molars the tendency increases in a posterior direction, while in the lower teeth M_1 seems to be the most affected, with an average of 0·9 of a cusp per tooth, the corresponding average for M_2 and for M_3 being 0·6. Furthermore, 7 *ectostylids* were routinely recorded because of their big size: all of them were observed on M_1. *Entostyles* and corresponding *ectostylids* are the most frequently occurring secondary cusps: they represent 36·1% and 29·6% of the total respectively.

CHAPTER 5

DIMENSIONS OF THE TEETH

A. Adult Dentition

From the maximum antero-posterior (mesio-distal) and transverse dimensions of each tooth, the ranges of variation have been established, as well as the mean and standard error (M + s.e.), the standard deviation (σ), and the coefficient of variation (V) (table 7). The data, as well as the indices, have also been expressed

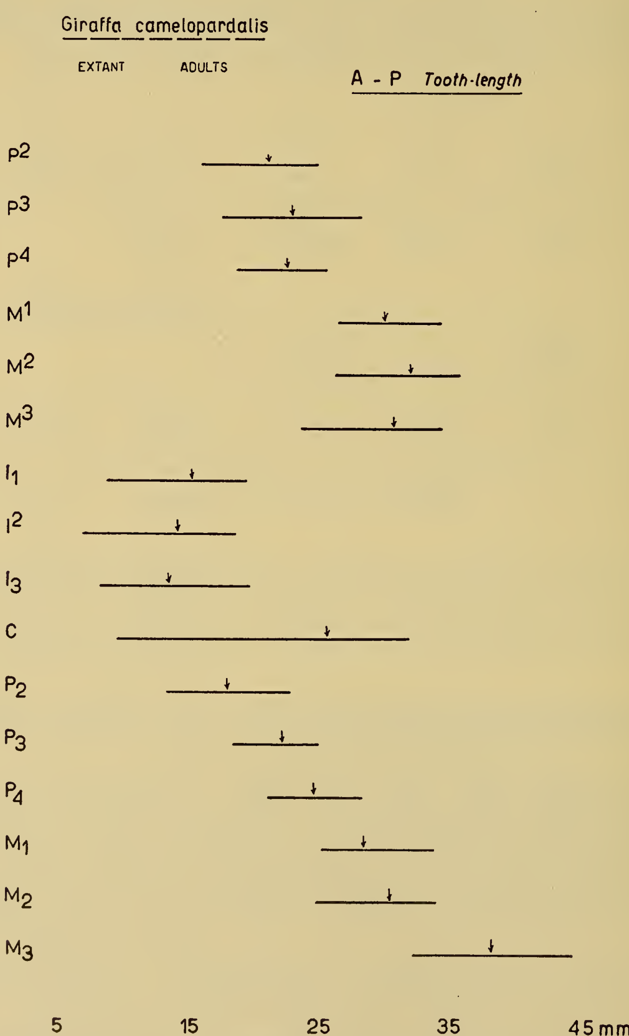

Fig. 7. The ranges of variation of the A–P length of the permanent teeth in *Giraffa camelopardalis*. ↓ = the mean value.

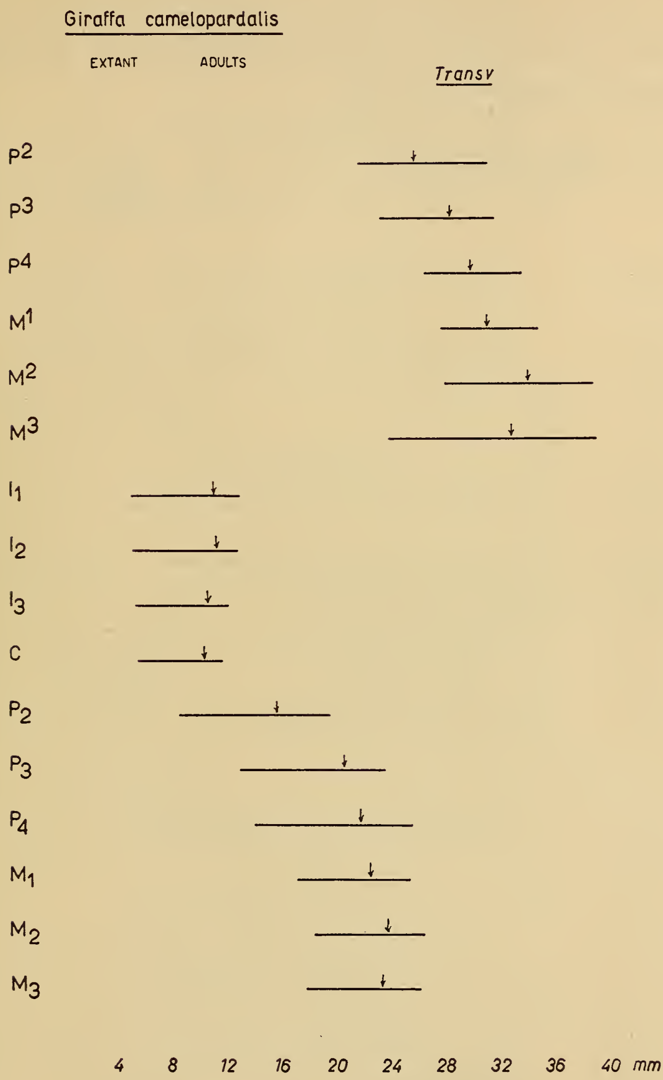

Fig. 8. The ranges of variation of the transverse diameter (breadth) of the permanent dentition.
↓ = mean value.

in graphic form (figs. 7, 8 and 9). It may be observed from the mean and from the relative dimensions of the teeth (fig. 10), that there is a decreasing gradation of size for the postcanine teeth from back to front, except for M2 which is in general longer (A–P) in the upper jaw, and broader in both jaws, than M3. The decrease in size of the teeth in both upper and lower jaw is gradual, except for P2, which is relatively much smaller than P3 (more in the lower than in the upper). In the family Giraffidae, P1 has disappeared, while the unusual decrease in relative size observed in P2, linked with the fact that in some specimens it is also absent (see chapter 3), may suggest an eventual disappearance of P2.

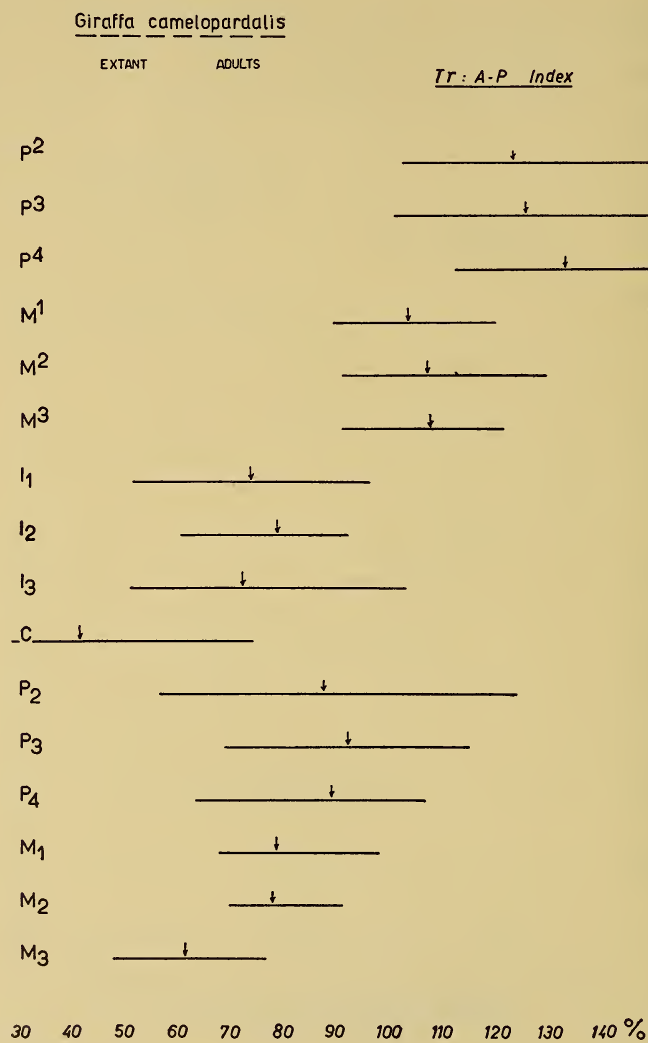

FIG. 9. The ranges of variation of the transverse/A–P index of the permanent dentition.
↓ = mean value.

Both the premolars and the molars of the upper jaw tend towards a square shape, the breadth being normally even greater than the A–P length (fig. 10). In table 7 (and fig. 9) this is indicated by the fact that the mean of the transverse/A–P

Tooth	A — P (mm.)					Transverse (mm.)					Transv./A — P Index				
	N	M + s.e.	Range of Variation	σ	V	N	M + s.e.	Range of Variation	σ	V	N	M + s.e.	Range of Variation	σ	V
I_1	50	15·00±·326	8·6—19·2	2·31	15·46	49	10·92±·202	4·9—12·8	1·42	13·00	48	73·34±1·278	52·1— 97·0	8·86	12·08
I_2	51	14·00±·301	6·8—18·3	2·15	15·35	50	11·08±·176	5·0—12·6	1·25	11·28	50	78·69±1·210	60·9— 94·0	8·56	10·87
I_3	42	13·36±·376	8·5—19·5	2·44	18·26	43	10·48±·180	5·2—12·0	1·18	11·25	46	71·91±1·460	50·7—103·0	9·90	13·77
C	49	25·39±·688	9·5—31·7	4·82	18·98	50	10·24±·181	5·4—11·5	1·28	12·50	47	41·02±1·176	28·6— 70·4	8·06	19·64
P_2	109	17·80±·203	13·3—22·6	2·12	11·92	109	15·57±·225	8·4—19·4	2·35	15·09	109	87·41±1·100	56·5—124·0	11·55	13·21
P_3	125	22·06±·149	18·4—24·8	1·65	7·47	124	20·53±·191	12·9—23·5	2·13	10·37	124	91·95± ·801	68·8—115·0	8·90	9·67
P_4	126	24·54±·144	21·0—28·1	1·62	6·60	126	21·76±·156	14·0—25·5	1·88	8·62	126	89·02± ·602	63·7—106·9	6·75	7·58
M_1	148	28·36±·145	25·1—33·7	1·78	6·27	142	22·27±·120	17·1—25·3	1·43	6·42	143	78·59± ·432	67·9— 98·1	5·15	6·55
M_2	136	30·32±·155	24·7—33·9	1·80	5·93	133	23·61±·123	18·3—26·4	1·42	6·01	135	77·77± ·355	69·7— 90·9	4·12	5·29
M_3	126	38·16±·228	32·1—44·3	2·56	6·70	120	23·30±·168	17·7—26·1	1·84	7·89	120	61·21± ·445	47·6— 76·4	4·90	8·00
P^2	126	20·78±·141	15·8—24·6	1·58	7·60	117	25·59±·181	21·5—30·7	1·96	7·65	117	122·86± ·856	104·0—149·0	9·25	7·52
P^3	128	22·60±·141	17·3—27·9	1·60	7·07	118	28·12±·160	23·1—31·4	1·73	6·15	118	125·12± ·772	101·0—156·8	8·42	6·73
P^4	123	22·24±·128	18·4—25·3	1·41	6·33	115	29·65±·147	26·3—33·1	1·58	5·32	115	132·86± ·763	114·0—158·4	8·17	6·16
M^1	141	29·71±·166	26·2—33·5	1·97	6·63	136	30·91±·166	27·5—34·6	1·93	6·24	136	103·91± ·507	88·0—119·4	5·94	5·71
M^2	137	31·72±·178	26·0—35·4	2·09	6·58	131	33·83±·167	27·8—38·5	1·91	5·64	130	106·79± ·495	91·6—128·0	5·60	5·24
M^3	126	30·41±·188	23·5—34·1	2·26	7·43	122	32·62±·207	23·7—38·9	2·28	6·98	121	107·44± ·629	91·5—122·4	6·92	6·44

TABLE 7. Dimensions of teeth of modern adult *Giraffa camelopardalis*.

index is greater than 100. On the other hand, in the lower jaw, the A–P length is always greater than the breadth, so that the teeth tend to be rectangular in their longitudinal axis.

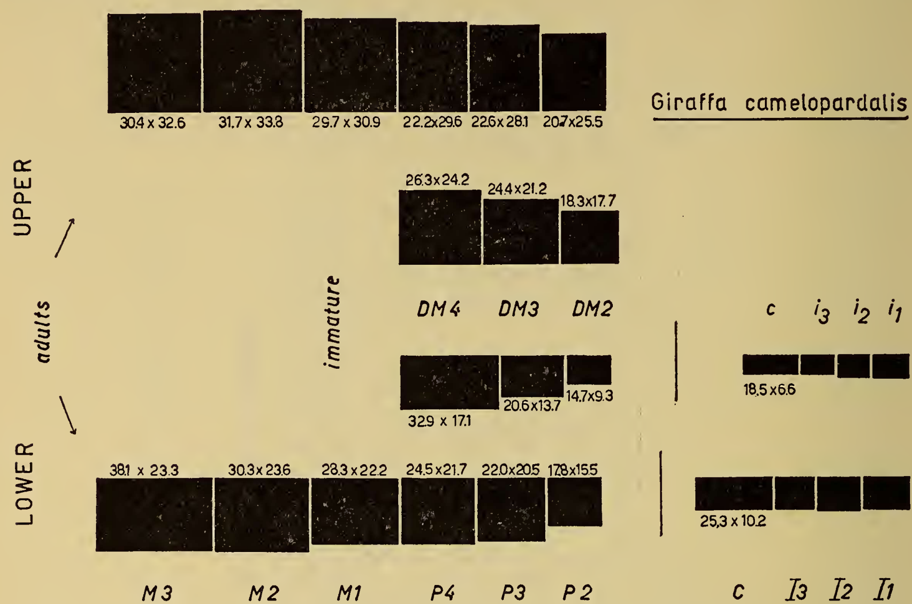

Fig. 10. Graphic representation of the relative ranges of dimensions (A–P length and breadth) of adult and milk (immature) dentitions. Mean dimensions are indicated.

Although similar in breadth to the incisors, the canine is approximately twice the length of each incisor, probably because of its bilobate nature. The incisors show a decreasing length (A–P) from front to back, although they have approximately the same breadth.

Index		N	*Range of Variation*	M	s	V
Length	$\frac{P^2}{P^3}$	122	73·8—109·2	91·94±0·527	5·86	6·37
Breadth	$\frac{P^2}{P^3}$	106	74·0—104·8	91·28±0·429	4·38	4·79
Index	$\frac{\text{Transv./A–P } P^2}{\text{Transv./A–P } P^3}$	105	84·0—131·2	99·98±0·841	8·58	8·58
Length	$\frac{P^3}{P^4}$	121	84·9—124·0	101·60±0·572	6·30	6·20
Breadth	$\frac{P^3}{P^4}$	109	79·6—105·9	95·02±0·373	3·88	4·08
Index	$\frac{\text{Transv./A–P } P^3}{\text{Transv./A–P } P^4}$	109	70·8—111·6	94·19±0·653	6·80	7·21
Length	$\frac{P_2}{P_3}$	109	56·2— 94·8	80·40±0·746	7·76	9·65

Index		N	*Range of Variation*	M	s	V
Breadth	$\frac{P_2}{P_3}$	110	57·7— 98·8	76·70±0·665	6·92	9·02
Index	$\frac{\text{Transv./A–P } P_2}{\text{Transv./A–P } P_3}$	109	74·2—130·0	95·84±1·042	10·84	11·31
Length	$\frac{P_3}{P_4}$	123	77·8—103·1	90·23±0·396	4·36	4·83
Breadth	$\frac{P_3}{P_4}$	116	68·8—105·0	93·17±0·570	6·10	6·54
Index	$\frac{\text{Transv./A–P } P_3}{\text{Transv./A–P } P_4}$	121	78·8—128·4	103·64±0·781	8·60	8·29
Length	$\frac{M^1}{M^2}$	127	80·5—101·6	93·12±0·348	3·90	4·18
Breadth	$\frac{M^1}{M^2}$	121	81·3— 98·8	91·44±0·320	3·52	3·84
Index	$\frac{\text{Transv./A–P } M^1}{\text{Transv./A–P } M^2}$	120	84·8—108·9	98·12±0·412	4·50	4·58
Length	$\frac{M^2}{M^3}$	122	84·6—140·8	104·13±0·665	7·32	7·02
Breadth	$\frac{M^2}{M^3}$	116	92·2—119·0	104·12±0·413	4·41	4·23
Index	$\frac{\text{Transv./A–P } M^2}{\text{Transv./A–P } M^3}$	114	81·7—117·9	100·15±0·618	6·56	6·55
Length	$\frac{M_1}{M_2}$	135	74·8—106·0	93·76±0·415	4·82	5·14
Breadth	$\frac{M_1}{M_2}$	134	83·9—101·8	94·38±0·276	3·18	3·36
Index	$\frac{\text{Transv./A–P } M_1}{\text{Transv./A–P } M_2}$	133	88·9—127·8	100·99±0·520	5·98	5·92
Length	$\frac{M_2}{M_3}$	125	69·8— 95·4	79·58±0·421	4·68	5·88
Breadth	$\frac{M_2}{M_3}$	120	87·1—133·4	101·34±0·372	4·06	4·00
Index	$\frac{\text{Transv./A–P } M_2}{\text{Transv./A–P } M_3}$	120	109·0—150·5	127·38±0·782	8·52	6·68
Breadth	$\frac{P^3}{M^1}$	108	73·6—106·2	91·03±0·469	4·84	5·31
Breadth	$\frac{P^4}{M^1}$	108	83·0—109·5	95·74±0·458	4·72	4·93
Length	$\frac{P_4}{M_2}$	124	69·0— 89·6	80·96±0·388	4·31	5·32
Breadth	$\frac{P_4}{M_2}$	121	76·6—104·2	92·62±0·485	5·34	5·76

TABLE 8. Dental Index for lengths and breadths, as well as the index for the transv./A–P ratios of successive permanent teeth of *G. camelopardalis*.

The ratios of the length and of the breadth of successive postcanine teeth (P2/P3, P3/P4, M1/M2, M2/M3) are expressed as the 'Dental Index' for premolars and molars. For both their lengths and breadths, the range of variation, mean, standard error, standard deviation and coefficient of variation were determined (table 8, fig. 11). In addition, the ratios of the transverse/A–P dimensions have been compared and expressed as an Index. This data has proved particularly valuable in assisting the authors to determine the diagnosis of isolated fossil teeth. In this respect, the ratios of the breadths of P^3/M^1, P^4/M^1, P_4/M_2, and of lengths of P_4/M_2 have also been helpful (table 8).

B. Deciduous Dentition

The measurements of 331 milk-teeth are summarized in table 9 and figs. 10, 12. It is clear that the front teeth (incisors and canines) and the first molar, both in the mandible and the maxilla, have the largest coefficient of variation, while the postcanine teeth show much less variation of both length and transverse breadth. In most of the cases, the breadth seems to be slightly less variable than the length.

Tooth	A–P (mm.)					Transverse (mm.)				
	N	Range of Variation	M	σ	V	N	Range of Variation	M	σ	V
i_1	23	9·5—13·5	11·53±·225	1·08	9·36	22	6·0— 8·2	7·48±·127	0·60	8·02
i_2	24	7·2—13·5	11·27±·308	1·51	13·39	23	5·7— 8·2	7·22±·133	0·64	8·86
i_3	27	7·7—18·8	10·85±·219	1·14	10·50	26	5·0— 7·7	6·67±·149	0·76	11·39
c	30	13·8—21·4	18·54±·285	1·56	8·41	30	4·7— 8·4	6·64±·135	0·74	11·14
DM_2	37	12·2—19·8	14·75±·291	1·77	12·00	37	7·2—11·7	9·35±·182	1·11	11·87
DM_3	38	18·0—24·1	20·64±·230	1·42	6·87	36	11·7—15·7	13·72±·155	0·93	6·77
DM_4	39	28·0—35·9	32·99±·227	1·42	4·30	37	15·1—18·9	17·14±·171	1·04	6·06
DM^2	36	16·0—20·4	18·37±·240	1·44	7·83	36	16·3—19·5	17·79±·193	1·16	6·44
DM^3	38	22·2—27·2	24·47±·209	1·29	5·27	38	19·3—23·1	21·23±·162	1·00	4·72
DM^4	38	24·3—29·0	26·33±·191	1·18	4·48	38	21·3—26·3	24·28±·189	1·17	4·82

Table 9. Summary of measurements of 331 milk teeth. (N = number of specimens; M = mean given with standard error; σ = standard deviation; V = coefficient of variation).

The breadth/length index has also been calculated (table 10). Here again, the front teeth and first lower molar show a very high degree of variation, reaching 17·8%. The data indicate that all the milk teeth are longer than broader, the ratio being close to 100% for the upper molars. They are all relatively longer than the corresponding permanent teeth (fig. 10), and this feature is responsible for the lower index (table 10).

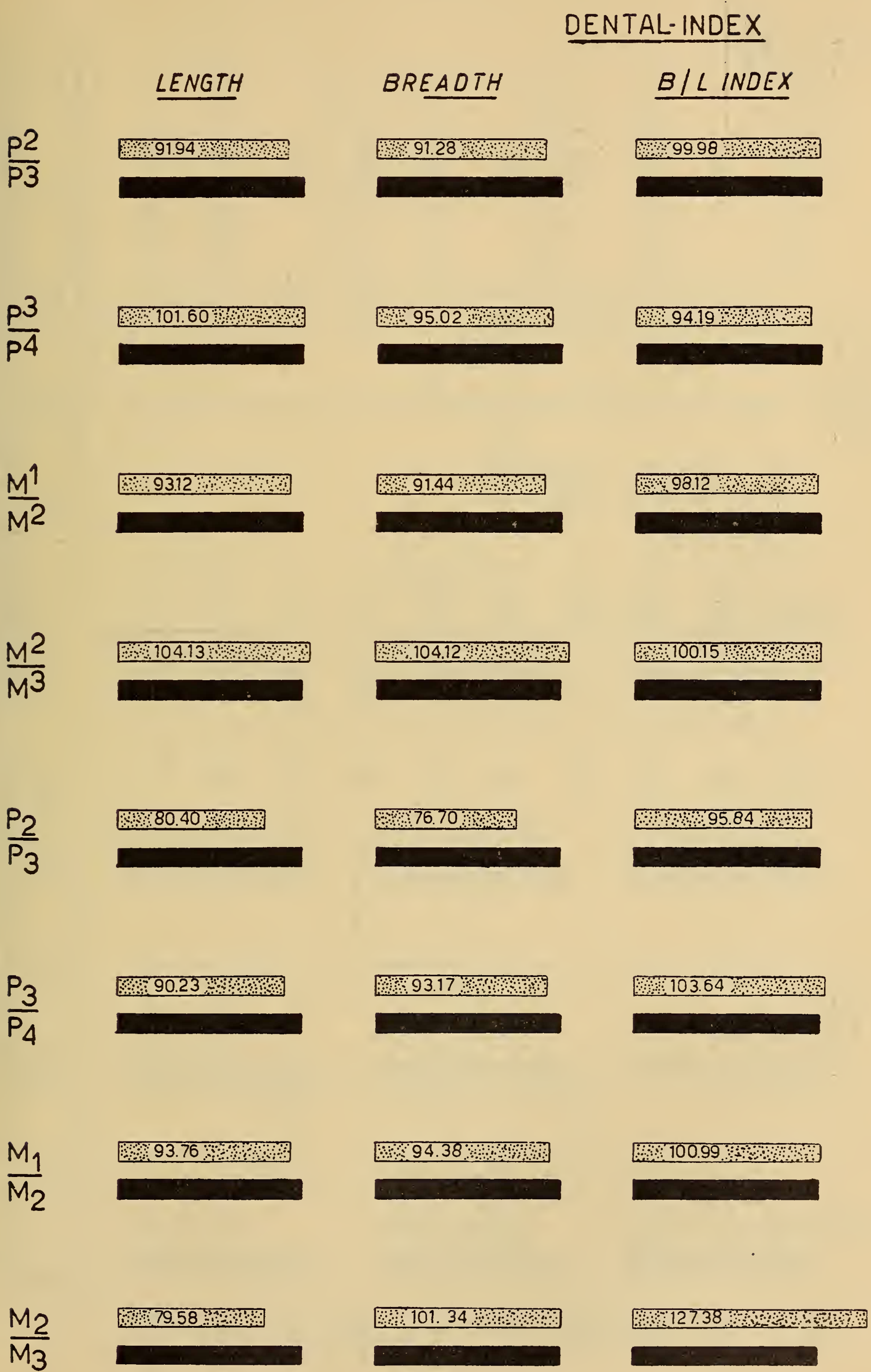

FIG. 11. Ranges of variation of the Dental Index for length and breadth and of the breadth/length index of permanent teeth in *Giraffa camelopardalis*. Mean values are indicated.

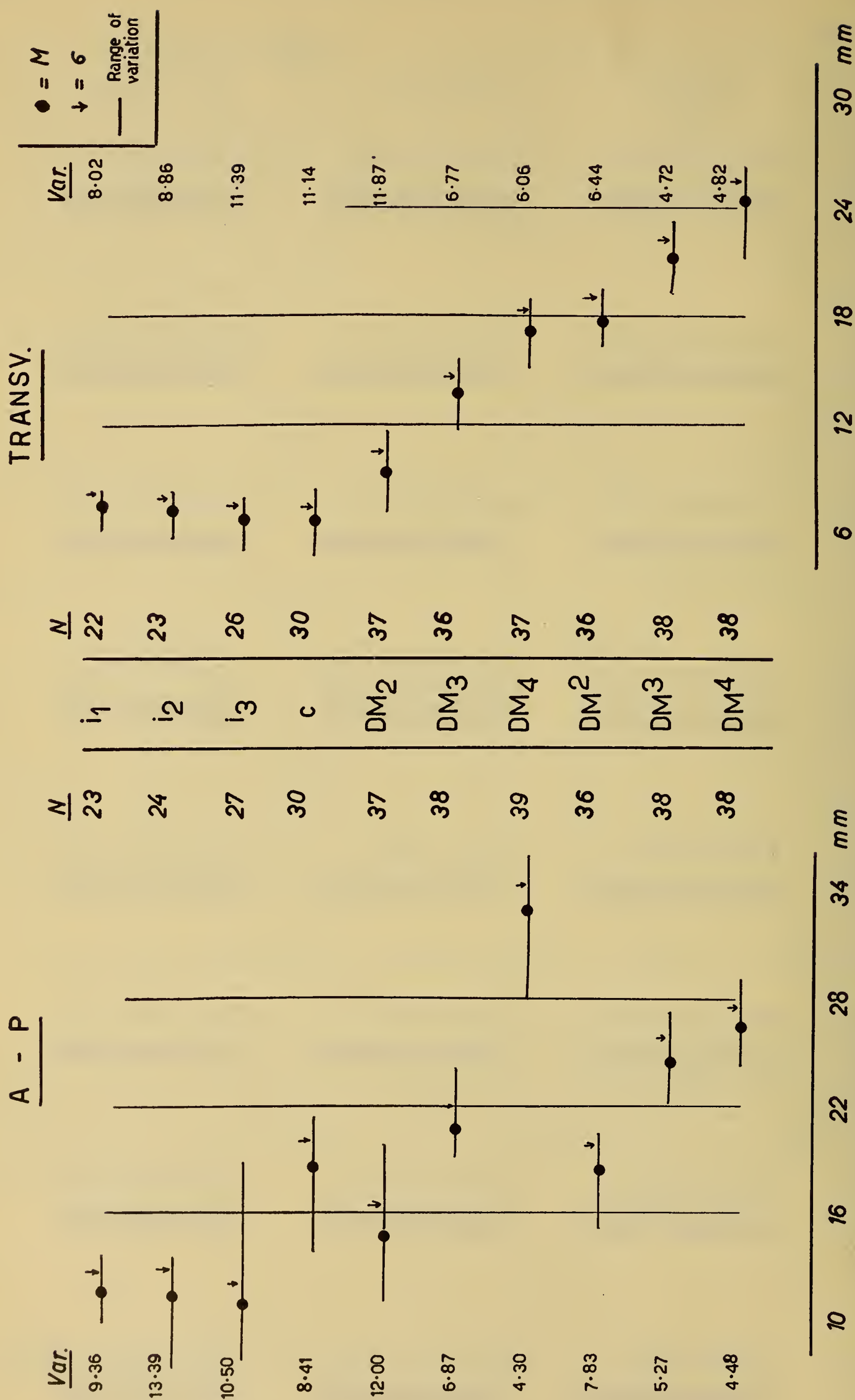

Fig. 12. Graphic representation of the ranges of variation (——), mean (●), standard deviation (↓), and coefficient of variation (*var.*) of the A–P and transverse dimensions of milk (deciduous) teeth in *Giraffa camelopardalis*.

Tooth	N	Range of Variation	M	σ	V	M in corresponding permanent tooth
i_1	22	52·2— 80·1	66·14±1·149	6·80	10·28	73·34
i_2	23	48·7— 97·0	65·26±2·187	10·48	16·05	78·69
i_3	26	41·3— 81·4	62·62±1·603	8·16	13·03	71·91
c	29	24·2— 44·8	35·78± ·680	3·66	10·22	41·02
DM_2	37	41·9— 91·2	64·44±1·894	11·52	17·87	78·59
DM_3	36	52·6— 78·2	66·58±1·086	6·52	9·79	77·77
DM_4	37	46·2— 58·0	52·30± ·509	3·10	5·92	61·21
DM^2	35	86·5—106·6	96·68±1·035	6·12	6·33	103·91
DM^3	38	78·8— 96·0	86·96± ·699	4·31	4·95	106·79
DM^4	38	82·0—101·0	92·28± ·741	4·57	4·95	107·44

TABLE 10. Breadth/Length (Transverse/A–P) Index of 331 milk teeth, compared with the same index in the corresponding permanent teeth. (N = number of specimens; M = mean, given with standard error in milk teeth; σ = standard deviation; V = coefficient of variation).

The 'Dental Index' has also been determined for the immature teeth (table 11, fig. 13).

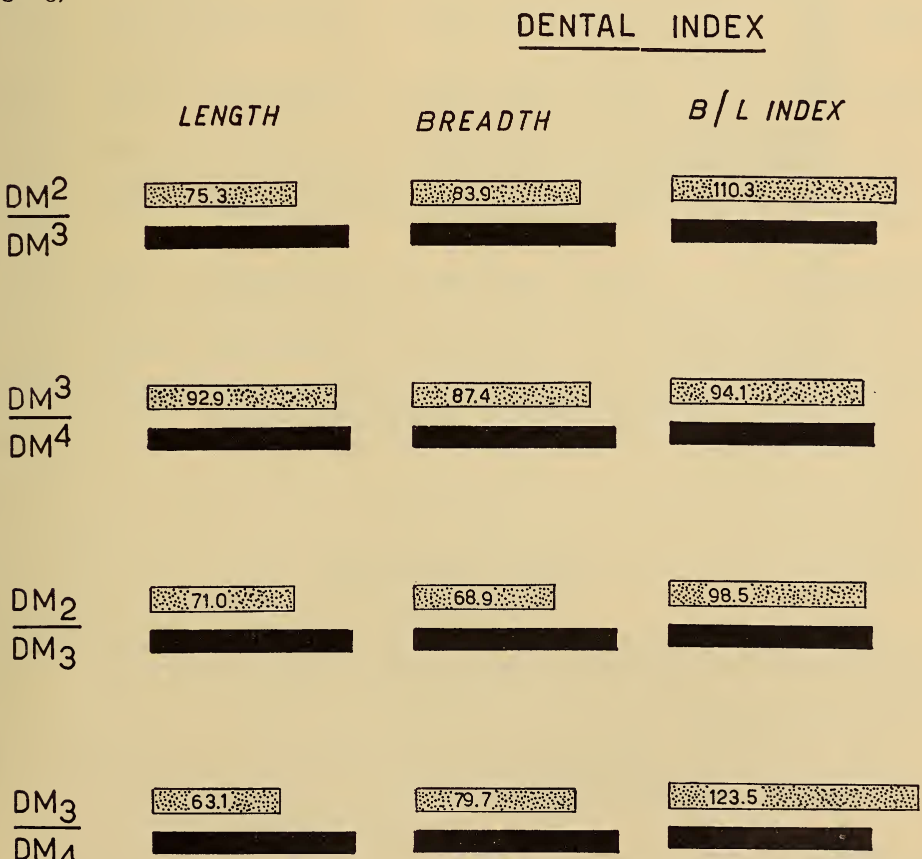

FIG. 13. Ranges of variation of the Dental Index for length and breadth and of the breadth/length index of deciduous teeth in *Giraffa camelopardalis*. Mean values are indicated.

Index		N	Range of Variation	M	s	V
Length	$\frac{DM^2}{DM^3}$	36	62·7– 81·9	75·38±0·811	4·87	6·46
Breadth	$\frac{DM^2}{DM^3}$	36	75·5– 92·3	83·94±0·678	4·07	4·84
Index	$\frac{\text{Transv./A–P } DM^2}{\text{Transv./A–P } DM^3}$	35	94·0–127·4	110·34±0·629	3·72	3·37
Length	$\frac{DM^3}{DM^4}$	38	85·7–102·2	92·93±0·545	3·36	3·61
Breadth	$\frac{DM^3}{DM^4}$	38	82·4– 92·7	87·47±0·472	2·91	3·32
Index	$\frac{\text{Transv./A–P } DM^3}{\text{Transv./A–P } DM^4}$	38	85·5–101·7	94·11±0·735	4·53	4·81
Length	$\frac{DM_2}{DM_3}$	37	54·6– 96·3	71·05±0·983	5·98	8·41
Breadth	$\frac{DM_2}{DM_3}$	35	56·2– 80·2	68·95±0·991	5·86	8·49
Index	$\frac{\text{Transv./A–P } DM_2}{\text{Transv./A–P } DM_3}$	35	63·7–134·2	98·54±3·113	18·40	18·67
Length	$\frac{DM_3}{DM_4}$	38	55·6– 72·3	63·11±0·581	3·58	5·67
Breadth	$\frac{DM_3}{DM_4}$	36	70·2– 92·1	79·73±0·821	4·93	6·18
Index	$\frac{\text{Transv./A–P } DM_3}{\text{Transv./A–P } DM_4}$	36	98·7–144·0	123·52±1·760	10·56	8·54

TABLE 11. Dental Index for lengths and breadths, as well as the index for the transverse/A–P ratios of successive immature teeth of *Giraffa camelopardalis*.

CHAPTER 6

ROOT ANOMALIES

Root anomalies are by no means uncommon among recent giraffes. They will be dealt with in the adult dentition first, and then in the milk dentition.

I. Adult dentition

Three main types of anomalies have been observed: accessory roots, root reduction and root fusion.

A. Accessory roots

They are by far the commonest abnormality. Among the 62 adult specimens analysed, not less than 15 individuals (24%) show distinct accessory roots in a total of 38 teeth (table 12). The data indicate that the accessory roots are found exclusively in the last two lower premolars and in the lower molars, the incidence being much higher in M_2 and M_3.

Specimen	P_3		P_4		M_1		M_2		M_3	
	R	L	R	L	R	L	R	L	R	L
X_3	x									x
X_1								x		
24291					x	x				
27137							x	x		
27752							x	x	x	x
34425									x	x
34424		x					x	x	x	x
34426	?		?				?		?	
35536							x	x	x	x
51198		x			x				x	x
69403						x		x		x
83460		x								
139696							x	x		
154033							?			
251797									x	
TOTAL	≥5		≥1		4		≥14		≥14	

TABLE 12. Distribution of accessory roots in adults. (R = right, L = left. In two specimens, it has been impossible to tell from the records whether the anomaly affects the particular teeth bilaterally or not: a '?' indicates that the side is unknown).

The most common type is that of a small, thin and short root located between the two major anterior and posterior roots, either on the buccal or the lingual side. It never develops the flattened plate shape (side-to-side) of the two main roots. It is rather circular, hardly extending into the bony socket of the mandible. In some cases it is poorly developed, resembling a very small tubercle and projecting 2 or 3 mm. from the root base, forming a small depression in the alveolar border of the mandible. In this series the accessory root is always situated on the lingual side of the premolars and on the buccal side of the molars. On the premolars it occurs unilaterally, whereas—with very few exceptions—the accessory root is bilaterally situated on the molars when present. In these cases, the right molar presents the anomaly as the mirror image of the left corresponding tooth.

It is a debatable point whether this root is really an *accessory* root or whether it is just the result of some division or splitting off of one of the main roots. On one specimen only (27137), there is a definite indication of a bilateral division of the anterior root of M_2: on both teeth the anterior root is bifid, the distal branch being clearly situated under the protoconid. In all the other cases, however, the accessory root is central, situated under the protoconid-hypoconid junction, quite separate from the anterior and posterior main roots.

It is not possible to link in any way the molar accessory root with the presence of an ectostylid: among the 21 cases of molar accessory roots, only 13 correspond to specimens presenting any form of ectostylid. This does not indicate a significant correlation between accessory root and ectostylid, especially when one considers that in 86 molars presenting an ectostylid (table 6) there are only 13 which have an accessory root.

B. Root reduction

Root reduction has been observed in three cases only, all P_2. In these, the tooth has only one single root, round in section and rather conical in appearance, instead of the two normal (anterior and posterior) roots. The specimens are 34423, 34424 and 83460. On the former two, the reduction has only been observed unilaterally, the corresponding opposite tooth root being perfectly normal. Specimen 83460 has only one P_2 (right), the corresponding left premolar being congenitally absent. The measurement of the teeth concerned in the three specimens are compared with the mean and range of variation of 109 other P_2 specimens (table 13):

Specimen			A–P	Transverse	Transv./A–P Index
34423	R	(reduced root)	13·8	12·2	88·4
	L	(normal root)	18·9	15·9	84·0
34424	R	(normal root)	14·1	17·5	120·4
	L	(reduced root)	15·5	16·4	105·9
83460	R	(reduced root)	13·6	13·5	99·2
	L	(tooth absent)	—	—	—
Series of 109 *teeth*					
Mean			17·8	15·5	87·4
Range of variation			13·3—22·6	8·4—19·4	56·5—124·0

Table 13.

From these figures it may be inferred that, in two of the three observed cases, reduction of the root corresponds to an appreciable reduction in A–P diameter (viz. 22·5% and 23·6% in 34423 and 83460 respectively). The reductions in transverse diameter are 21·7% and 12·9% respectively: it is probably not very significant, especially in view of the negative reduction (—0·5) in 34424. Similarly, in these three specimens, the A–P measurement is situated at the lower limit of the range of variation, while the transverse breadth falls within the range of one sigma from the mean value. Comparing further the teeth with the reduced root with the opposite ones which have the normal root, there is a distinct correlation between reduction in root and in size of the crown in one case only (34423). On the other hand, it is remarkable that, with the exception of the above case, a reduction in size of the tooth does not seem to correspond to a reduction of the root.

C. Root fusion

One single case of root fusion has been noted: the M^3 in 53546 has (bilaterally) a bridge completely fusing the posterior buccal root with the lingual one along the total height of the roots.

II. Milk dentition

Root variation is frequently observed in the third lower milk molar DM_4. A total of 20 immature skulls, in which this tooth was still bilaterally *in situ* and sufficiently well preserved to allow observations, were studied. All the 40 DM_4 have three roots. The two main roots (anterior and posterior) are well developed, extending bucco-lingually, being rather flattened from side-to-side, and corresponding to the two extreme pillars of the deciduous molar, but they do not show a very high degree of variability. However, situated between them, there is constantly a third root, corresponding to the intermediate pillar. It is rather buccally located, circular in shape, and is shorter than the two main roots.

The development of this central root is quite variable. The normal appearance (so-called because it was observed in 28 out of 40 cases) is that of a cylindrical root, sufficiently long to penetrate the alveolar socket of the tooth where it is really 'rooted', although less than the other two main roots. This is the general rule for the left DM_4 (18 cases), and shows in only 10 of the cases on the right side of the mandible (table 14).

Variation	Right	Left	Total
'Normal'	10	18	28
Reduced *single* central root	1	1	2
Divided central root:			
2 normal rootlets	3		3
1 normal and 1 truncated	3		3
2 truncated	2	1	3
3 truncated	1		1
Total	20	20	40

Table 14. Variability in the central root of DM_4, and distribution in right and left teeth.

In one case, this central root was so small and reduced that it hardly indented the mandible, and could scarcely be called a real root, being not very unlike some of the accessory roots observed on the permanent molars or premolars (*vide supra*), although it was much thinner. In ten cases, however, the central root was bifid or multiple, possessing two or even three small thin rootlets parallel to each other and originating from the crown-root junction. Here again there appears to be a high degree of individual variation, and one could schematically summarize the observations by distinguishing three main types of 'multiple' central root: (i) a double central root, each of the two parallel rootlets being as long and as large as the normal single ones: (ii) in addition to the normal central root, and parallel to it, the second accessory root is much shorter and reduced, hardly reaching the bone where it is never well 'rooted'; (iii) two or even three small reduced rootlets are found, truncated and just reaching or hardly penetrating the alveolar border.

CHAPTER 7

APPEARANCE AND VARIATIONS OF THE HORN-CORES

Lydekker (1904) attempts to classify *Giraffa camelopardalis*, distributed over the vast geographical area from the Cape to the Sudan and Ethiopia, according to the colour and the blotching of the skin (see Introduction, page 375) and to the variation of the horns. He describes a gradual transition from south to north from a two-horned animal into one (so far as the males are concerned) with three horns, but he believes that this is by no means regularly progressive, for one finds in the eastern districts of the Continent a five-horned and even a six-horned 'race'. On this basis, Lydekker finds it possible to distinguish:

(*a*) seven subspecies of the Northern and Eastern giraffes which are all characterized by the development of a large frontal unpaired horn, namely, *typica* (in Nubia), *reticulata* (in Somaliland), *antiquorum* (in Kordofan), *cottoni* (in South Lago, Uganda), *rothschildi* (Baringo), *tippelskirchi* (Kilimanjaro) and *congoensis* (Congo);

(*b*) four other subspecies of the Western and Southern giraffes, whose frontal horn is rudimentary or even aborted, namely, *peralta* (Nigeria), *angolensis* (Angola), *wardi* (northern Transvaal), and *capensis* (Cape) (fig. 14).

The main paired horns are always present, but particularly well developed in *rothschildi* and still better in *wardi*. Posterior or occipital horns are very well developed in these two subspecies, but less in *cottoni*. No reliable information on these posterior formations was available for *tippelskirchi* and *angolensis*. An unusual 'azygous' orbital horn was described in *cottoni* and *rothschildi*, projecting horizontally outwards from the middle of the frontal border of the right and left orbit respectively. Lydekker's observations are summarized in the following table.

Subspecies	Anterior horns	Main pair of horns	Posterior horns	Additional or 'azygous'
typica	x	x	—	—
antiquorum	x	x	—	—
reticulata	x	x	?	—
cottoni	x	x smaller than in *rothschildi*	x smaller than in *rothschildi*	x on right orbit
rothschildi	x	x well developed	x well developed	sometimes; then on left orbit
tippelskirchi	x smaller than in *rothschildi*	x	?	—
congoensis	x	x	?	—
angolensis	x	x	?	—
wardi	x large, aborted	x well developed	x stronger than in *rothschildi*	—
capensis	x rudimentary	x	—	—
peralta	—	x	?	—

TABLE 15. Schematization of Lydekker's subspecific classification and horn distribution. (x = present; — = absent; ? = doubtful.)

Fig. 14. Map of Africa indicating the distribution of the subspecies of *Giraffa camelopardalis*, according to Lydekker's classification (1904).

Because of the large amount of material available to the authors, the following observations indicate that Lydekker's useful information must be somewhat revised.

The sexual difference is very marked in the horns which are usually poorly developed in females (fig. 15): thus it is hardly possible to make any subspecific classification on the basis of the horns. The median frontal horn does not exist in females, there being only a slight swelling on the frontal without development of the 'ossicone'. The main horns, which are always much smaller than in the males of the same catalogued subspecies, measure 8–15 cm. in length from tip to base, the diameter not exceeding 3 cm. They are cylindrical and smooth, pointed at their tip, and

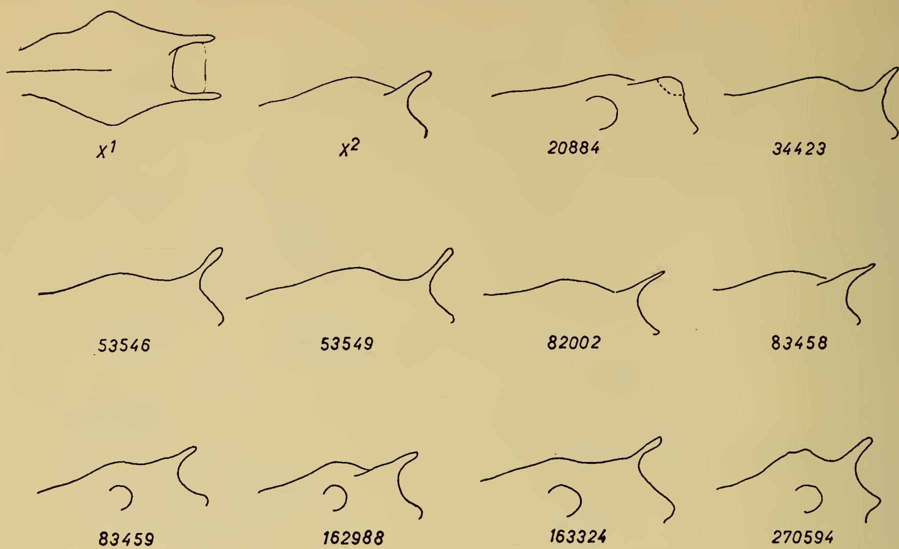

FIG. 15. Sketches showing portions of the skulls of female giraffes (*Giraffa camelopardalis*) indicating the major variations in the development of the horns. Lateral views, except X¹ which is *norma verticalis.*

usually constricted at their base. Posterior occipital horns and azygous horns were not found in the females.

FIG. 16*a*. Sketches of portions of skulls of adult male giraffes (*Giraffa camelopardalis*) showing major variations in the development of the horns. Views are either *norma lateralis* or *verticalis.*

Males show a better development of their horns (fig. 16*a*, *b*) and it is possible to notice important differences. But does the wide range of variation permit subspecific distinctions? In order to answer this question, each type of horn will be discussed separately.

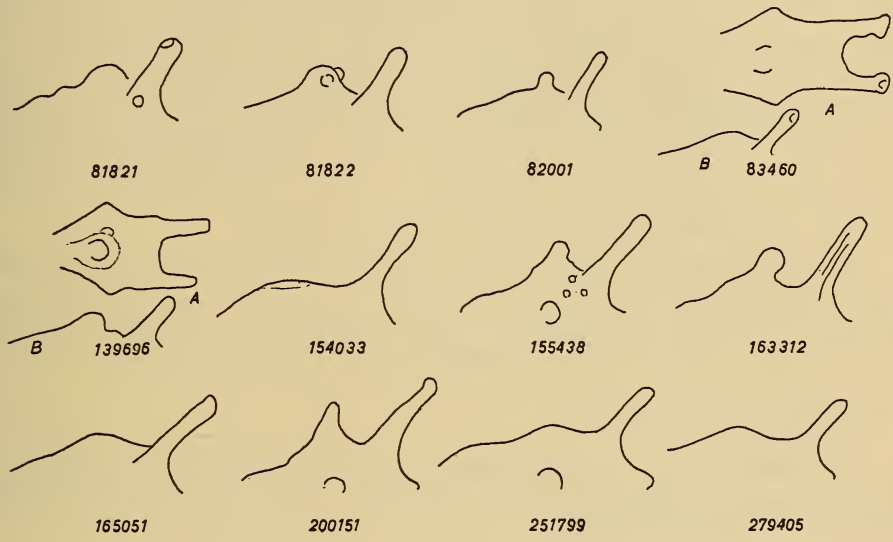

FIG. 16*b*. Further sketches of portions of skulls of adult male giraffes (*Giraffa camelopardalis*) showing major variations in the development of the horns. Views are either *norma lateralis* or *verticalis*.

A. SINGLE MEDIAN FRONTAL HORN

It varies from a simple swelling of the frontal (251799) to a true, very strongly developed horn (155438). The intermediate stages are observed as either a horny plate (154033), a slight eminence (279405), a globular formation (54123), or a rather large and regular cone (200151). Usually the anterior part of the horn has a more gentle slope (155438) which gradually extends on to the nasal bones. Very often on the median sagittal line, anteriorly, are one (155438), two (81821), three (27752), four (81820) or more (27137) smaller nodules; one or two may even be found on the side of the horn (139696) or on the top (81822 and 53765). The profile of the posterior part of the horn is mostly S-shaped (163312), so emphasizing its knob-like appearance. The whole formation is generally symmetrical on both sides of the sagittal plane. In one case however (27137), its transverse horizontal section looked like a crescent open anteriorly and to the right, with both extremities of the crescent converging towards a completely isolated smaller knob.

B. Pair of main horns

All the male giraffes have these two horns very well developed. The shape is commonly that of a rounded column, measuring 15–23 cm. in length, 4–6 cm. in breadth, and the diameter at the tip is 4–7 cm. A difference in size between right and left horn is by no means rare, the one being sometimes 35% longer than the other. Both horns are usually parallel: if not, their divergence from the base is hardly noticeable, so that the external interhorn breadth measured at their tips is always smaller than the external biorbital breadth. The angle formed by the horns with the Frankfort plane is very constant and in all the specimens where this could be measured, it ranged from 48° to 58°. The general shape of the horns is that of a column regularly cylindrical from the base upwards, and at the tip it forms a rounded knob (83460 and 24292). The tip is sometimes flattened (27137), the medial edge of which then projects more than the lateral one. In other cases the column maintains its regular circumference from base to tip (53550, 139696).

These fronto-parietal main horns are usually relatively smooth, having small, shallow vertical grooves, but they may possess a few marked axial ridges (163312 and 8371b), or display small knobs, in series of 2–5, forming irregular crests on the anterior (57675), medial (27752) or lateral (54123) margin of the horn.

C. Posterior occipital horns

The posterior 'horns' are much more a type of occipital crest or exostosis, condensed in two parallel eminences, than real horns. The crest is also very variable and may be completely absent.

D. Supplementary knobs

Smaller isolated supplementary knobs are not infrequently developed either on the lateral aspect of the frontal, between the posterior supra-orbital border and the base of the main horns (155438) when there are two or three concentrated in the same area, or on the orbital border itself (54123) when it is comparable to the azygous orbital horn described by Lydekker. But in the specimens studied it was distinctly *bilateral* and it is a *knob* rather than a 'horn projecting outwards horizontally'.

On the basis of the above results, the conclusions of Lydekker relative to the taxonomical significance of horn-shape and disposition are questionable. It is not impossible to find typical examples displaying the subspecific characteristics proposed by Lydekker: male 165051, for instance, from South West Africa, with big main horns (23 cm. in length) and a very rudimentary ossicone on the frontal. On the other hand, it is not difficult to find specimens which do not fit in his descriptions, e.g. 251799, registered as *G.c. tippelskirchi*, which certainly originated from Tanganyika, has no anterior horns and shows just a slight swelling of the frontal. Similarly specimens 24292, 34422, 34425, 34426 and 83460 which are all males from Bechuanaland (Mababe Flats) definitely have a very well developed anterior horn even though they geographically belong to the group of Angola, northern Transvaal or Cape, which—according to Lydekker's description—should have no such a large horn. Specimens from British East Africa, identified on the basis of their skin as *G.c. rothschildi*, have very strong main horns (155438 and 200151) whose length, general pattern or morphological appearance could not differentiate them from *tippelskirchi*. Among both groups one finds long, regularly cylindrical and smooth horns, or shorter, plumper horns with knobs (163312 and 27752; 54123 and 251799). Lateral 'azygous' knobs are found in both types (27752, 54123 and 155438), but on the one skull from Uganda, which should be *G.c. cottoni*, no such knobs were found, as should have been expected from Lydekker's description.

Consequently, it would be reasonable not to attempt any subspecific determination of modern African giraffes on the basis of the horn-cores. This principle is extremely important, as will especially be indicated in the discussion on the horn-cores of the extinct giraffids.

SECTION II

THE FOSSILIZED GIRAFFIDS

Introduction

Fossilized giraffid material has been discovered at various sites in Africa, namely:

North Africa	Oran (St. Charles) (Pomel 1892);
	Bou Hanifia, Chaâchas (Reygasse, 1919–20);
	St. Arnaud (Arambourg, 1934, 1948);
	Garet (Garaet) Ichkeul (Arambourg, 1949);
	Douaria (Roman and Solignac, 1934);
	Djebel M'dilla (Arambourg, 1952).
Egypt	Wadi Natrun, Garet-el-Mulùk (Stromer, 1907);
Sudan	Abu Hugar (Bate, 1951).
East Africa	Omo (Arambourg, 1947);
	Serengeti (Dietrich, 1937, 1942);
	Olduvai and Kagua (Hopwood, 1934, 1936);
	Olorgesailie, Kanam and Rawi (Leakey, 1951).
South Africa	Vaal River (Haughton, 1922);
	Florisbad (Dreyer and Lyle, 1931);
	Cornelia and Tierfontein, near Port Allan (van Hoepen, 1932);
	Makapansgat (Cooke and Wells, 1947; Broom, 1948);
	Hopefield (Singer, 1954);
	some unknown place, probably from the Vaal River gravels (Cooke, 1949).

Nearly all the above-mentioned material have been either assembled in Cape Town on loan for study, or examined in the respective Museums where the specimens are housed. In addition, for comparative purposes, an extensive survey of the giraffid material from the Siwaliks was carried out in the American Museum of Natural History (New York) and the British Museum (Natural History), London. It was not possible to obtain the original specimens previously described from the following sites outside Africa:

Greece	Velès (Schlosser, 1921);
	Pikermi (Gaudry, 1861, 1867);
	Samos, Salonique (i.e. Bounardja and Vatelük) (Arambourg and Piveteau, 1929).
U.S.S.R.	Taraklia (Khomenko, 1913).
Hungary	Baltavar (Pethö, 1885);
	Polgárdi (Kormos, 1911).
France	Mont Lébéron (Vaucluse) (Gaudry, 1873).
Turkey	Adrianople (Abel, 1904);
	Maragha (de Mecquenem, 1924).

In respect of the latter group of specimens all the available literature was studied. All the original material (from Africa) examined will be described according to geographic distribution.

CHAPTER I

OLDUVAI (OLDOWAY) GORGE, TANGANYIKA

A. Geology

The history and the geology of the enormous Olduvai Gorge (fig. 17(*a*), (*b*)) have been recorded by Leakey and by Reck, respectively (Leakey, 1951). Five beds are described: Bed I was deposited at the beginning of the East African Middle Pleistocene (early Kamasian), Beds II and IV correspond to the Kamasian and Kanjeran pluvials respectively, the Beds III and V represent the dry inter-pluvial and the post-Gamblian periods respectively. Giraffid remains have been recovered from Beds I–IV, although most of the material comes from Bed II (*vide infra*).

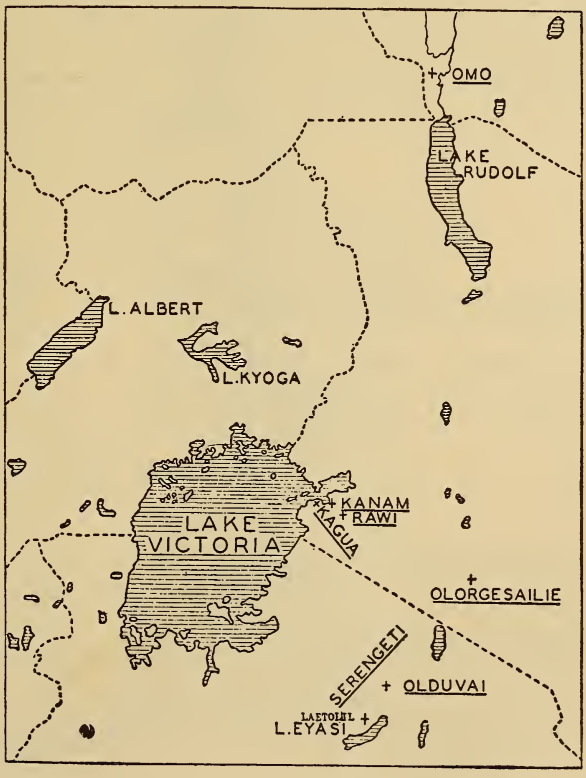

Fig. 17*a*. Map of Central-East Africa indicating some of the more important fossil sites.

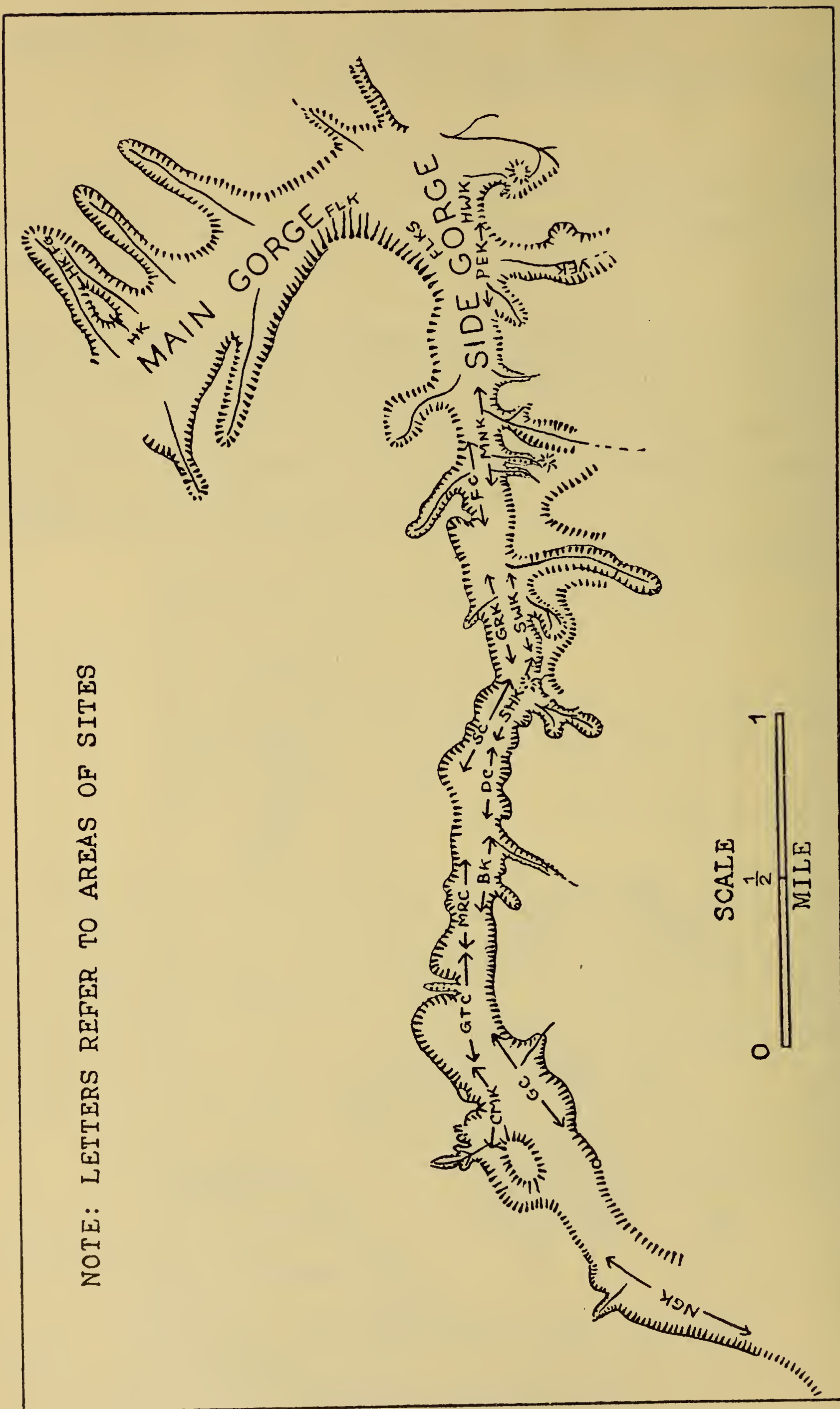

Fig. 17*b*. Map of Olduvai Gorge indicating designations of various sites (from Leakey, 1951).

B. The Material

The material recovered consists of loose teeth, or fairly complete dentitions, postcranial bones (mainly incomplete) and so-called 'antlers' (horn-cores).

1. *Previously described.* Hopwood (1934) described a right fourth lower premolar (M 14200) as the holotype of *Helladotherium olduvaiensis* sp. n., and as paratypes he mentioned a rolled fragment of a right mandibular ramus with P_4–M_1 (M 14686, horizon unknown) and a partial hind-limb (M 14687, Bed I). With the discovery of *Sivatherium*-like 'palmated antlers' (inverted commas, ours) from Bed II Olduvai (M 14954–14955) and from Kagua (M 14956), Hopwood (1936) referred the above material to *Sivatherium olduvaiense.* However, Dietrich (1937) stated that on the basis of a metacarpal (E. 122) which he had studied, he had already referred the Olduvai material to the Sivatheriinae (although he does not state whether this was ever published).

2. *Observations on material housed in the Coryndon Museum (Nairobi).* Material was kindly sent on loan by Dr. L. S. B. Leakey, Curator of the Coryndon Museum, and in addition horn-cores and postcranial remains from Olduvai were also studied in the British Museum (Natural History) and in the Coryndon Museum (Nairobi). Each specimen is described in detail, the specimen being numbered according to the museum registers, and the information given below with each number is found written on each specimen. The inscriptions have the following interpretation:

Old.	Olduvai Gorge.
Oldy.	Olduvai (Oldoway) Gorge.
BK	Indication of the site (see fig. 17(*b*)).
II	Bed II.
1951, 1952, etc. ..	Collected during those seasons.
S	The specimen has been found on the surface of the Bed referred to, but it does not necessarily belong to that Bed.
M	Before a number indicates registration by British Museum (Nat. Hist.).
Marsabit Road ..	A site about 100 miles east of the southern point of Lake Rudolph in Kenya.

Coryndon Museum Giraffid Material

A. *Horn-cores*

86	Old. BK II 1952.
Old. 1.53 ..	(Provisional number given by Mrs. Coryndon, in 1956.)
Old. 2.53 ..	(*Idem.*)
Old. 1952 ..	SHK II BK II base (S).
M 14954*b* ..	Oldy. BK II S (13.V.35).
Old. 3.53 ..	(Provisional number given by Mrs. Coryndon in 1956.)
M 17027 ..	Oldy. BK II S (14.V.35).
M 17028 ..	Oldy. BK II S (14.V.35).
M 17029 ..	Oldy. BK II S (14.V.35).
M 14955 ..	(At present in British Museum (Nat. Hist.).)

B. *Fragments of jaws*

Upper:

F 3655 .. Right maxilla, M^1—M^3, Old. II, 1941, *in situ.*

Lower:

6	Right mandible, P_2-M_3, Old. BK II.
F 3656 ..	Left mandible, M_1-M_3, Old. II.
1	Right mandible, P_4-M_3, Old. BK II.
365	Right mandible, M_1-P_3, Old. SKH II, 1953.
392	Right mandible, M_2, Old. SHK II, 1953.
3	Right mandible, M_3, Old. BK II.
93	Left mandible, M_1-M_3, Old. BK II, 1952.
92	Left mandible, M_2-M_3, Old. BK II, 1952.
91	Left mandible, M_1-M_2, Old. BK II, 1952.
Nguntiri site .	Left mandible, M_1-M_3, Old. BK II East 1953.
321	Left mandible, M_2-M_3, Old. BK II, 1953.

C. *Isolated teeth*

Upper:

premolars..	F 2989	?P^3, Oldoway 1941 II, *in*
molars ..	F 2993	M^2, Old. II.
	4	M^3, Old. BK II.
	109	M^3, Old. BK II, 1955
	F 2992	?, Old. II *in situ.*

Lower:

canine ..	97	Old. BK II, 1952.
premolars..	F 2991	P_4, Old. I S, 1941.
	2	P_4, Old. BK II.
	5	P_4, Old. BK II.
	7	P_4, Old. BK II.
	96	P_4, Old. BK II, 1952.
molars ..	105	M_1, Old. BK II, 1953.
	132	M_1, Old. BK II, 1953.
	95	M_2, Old. BK II, 1952.
	120	M_3, Old. BK II, 1955
	—	M_3, Marsabit Road.

Fragments of molars, further unidentifiable

166	Old. BK II, 1955.
116	Old. BK II, 1953.
8	Old.
100	Old. BK II, 1953.
98–99	Old. BK II, 1952.
—	Marsabit Road.
—	Olduvai surface.

D. *Post-cranial skeletal remains*

Forelimb:

116*p*.. ..	Proximal end of ulna.	Old. BK II, 1952.
115	Distal end of radius.	Old. BK II, 1952.
341	Os magnum.	Old. BK II, 1952.
114	Distal end of metacarpal.	Old. BK II, 1952.

Hindlimb:

100	Distal end of femur.	Old. BK II, 1952.
101, 112 ..	Distal end of tibia.	Old. BK II, 1952.
103, 108 ..	Calcaneum.	Old. BK II, 1952.
102, 107 ..	Astragalus.	Old. BK II, 1952.
104, 109, 110	Cubonaviculare.	Old. BK II, 1952.
105, 110A ..	Cuneiform.	Old. BK II, 1952.
106, 111 ..	Proximal end of metatarsal.	Old. BK II, 1952.
314	Distal end of metatarsal.	Old. BK II, 1953.
M 14687 ..	Almost complete articulated hindlimb, in B.M.(N.H.).	

Proximal phalanges:

113 ..	Old. BK II, 1952.
185 ..	Old. BK II, 1953.

F 3297 .. Old. S II.
F 364 .. Old. S I, 1941.
F 365 ..
— .. .. Old. surface.

Sesamoid bone:
342 .. Old. II, 1952.

Description of Specimens

A. Horn-cores

86. *Old. BK II* 1952 (plate 1(*b*), (*f*)).

This is a right horn-core. The base is hollow, extending about 170 mm. in depth from the broken edge. In section it is roughly triangular, the rounded apex being posterior. This posterior border becomes increasingly rounded towards the tip, while the more anterior region, rounded at the base, narrows to a well-defined border towards the apex. The anterior surface has knobs on it.

The medial surface is convex, both transversely and medio-distally, and presents deep grooves. Three of these are parallel to each other and to the convex anterior border, along which they run, even on to the knobs, following their profiles. Two other grooves are some distance from the anterior border, passing parallel to each other upwards and towards the posterior border.

There is also a short, very broad, oblique groove which leaves the base at the anterior convex border and runs obliquely upwards and backwards on the medial aspect.

The general curvature and the rotation (twist or torsion) of the horn-core are not marked: it is almost straight.

No flange* is visible. This portion has been reconstructed in plaster but it would appear unlikely that a flange would have been present. The first visible knob has been called knob 2.

This specimen is very similar to the horn-core from Garet Ichkeul (see Section III, chapter 1).

Length along posterior (concave) border: 710
Length along anterior (convex) border: 810
Height of the knobs: 20-40

	Circumference	*A–P*	*Breadth**
At base	415	150	114
Just under knob 2	350	128	
At knob 2		145	89
Just under knob 3	330	119	
At knob 3		130	83
Just under knob 4	300	113	
At knob 4		135	78
Just under knob 5	280	106	
At knob 5		110	64
At 'tip' (broken)		75	63

(* Side-to-side diameter.)

Table 16. Measurements of Old. 86 (mm.).

* The term 'flange' is applied to the appearance often presented by the anterior border just above the base when it narrows, flattens and sweeps (flanges) outwards.

Old. 1.53 and **2.53** (plate 1(*c*), (*e*); 1 (*a*), (*d*)).

1.53 is a right horn-core and 2.53 a left. They are very similar to one another, although they may not belong to the same individual because the rotation (torsion) of the horns differ from each other, 1.53 rotating 90° anti-clockwise, while 2.53 rotates clockwise (normal) through 140° from base to tip. This indicates the tremendous variation in torsion between horns which are otherwise very similar. Both horns have a marked flange (267 mm. and 155 mm. in length respectively) which terminates superiorly in knob 2 above which there are three other knobs (3–5) along the antero-medial border. The flange of 2.53 is shorter than that of 1.53. On the flange of 1.53 there are four small knobs, the highest of which corresponds to knob 2. These are not present on the flange of 2.53. On both horns there is a knob opposite the middle of the flange, but it is situated on the posterior border somewhat medially. This knob is designated 'P' and may be compared with the blade-like projection which led Falconer (1868) and Abel (1904) to term the horn a tri-radiate antler.

In both specimens the anterior border first passes upwards and laterally from the base (where it is ill-defined) and at about the middle of the flange it swings towards the medial side. In this way the lower part of the horn develops its rotary twist, which is more obvious in 2.53. Thus the anterior border which at the base is really antero-lateral tends to twist to the antero-superior aspect of the horn, while the posterior border—which is postero-medial at the base—tends to become inferior at the tip. Furthermore, as a consequence of this torsion, the antero-medial surface (which has the marked grooves) comes to lie on the posterior aspect of the horn above the flange region.

In specimen 1.53 the postero-lateral surface has no grooves at all, while the antero-medial surface presents two grooves near the anterior border, both parallel to it, and both broad but not deep. The cranial fragment at the base of 1.53 contains a few shallow sinuses but does not display any sutures and it is not possible to assess the correct orientation of the horn to the skull. It would have been valuable to obtain an understanding of the position of the horn on the skull so as to determine whether the criteria the authors have utilized for 'siding' the horns are correct or not (see also Section III, chapter 1).*

The base of 2.53 is hollowed out to a depth of approximately 300 mm. from the broken edge. There are some sinuses present. The grooves resemble those of 1.53 but they are more numerous, there being four on this specimen.

Distances between the knobs	*1·53*	*2·53*
2—3	141	196
3—4	110	164
4—5	146	146

* At the galley-proof stage, Dr. L. S. B. Leakey reported to one of the authors (R. S). that a Sivatherine skull complete with attached horn-cores had just been discovered at Olduvai and that a note on it would soon be published by him.

Length of the flange	267	155
Length along anterior (convex) border	950	1010
Length along posterior (concave) border	840*	690

* A portion of skull attached to the horn is included in this measurement.

	Circumference		*A—P*		*Breadth**	
	1·53	*2·53*	*1·53*	*2·53*	*1·53*	*2·53*
At base	400	390	159	145	127	90
Middle of flange	410	420	154	172	79	81
At knob 2	380	410	145	165	84	89
Just under knob 3	300	290	105	101		
At knob 3	330	290	129	104	76	75
Just under knob 4	280	250	106	90		
At knob 4	290	260	113	97	67	63
Just under knob 5	270	250	99	97		
At knob 5	290	290	117	115	59	58
Tip	170	170	52	59	52	47

(* Side-to-side.)

TABLE 17. Measurements of 1·53 and 2·53 (mm.).

Old. 3.53 (plate 2)

This is a fragment of a left horn-core with part of the proximal portion missing. The tip and distal end are practically intact. At the base the flange is still present, ending in knob 2. Above this is a large knob 3, the only other knob on the anterior border.

The hollowed-out portion of the base is very narrow and extends about 130 mm. from the broken edge. On the antero-medial surface there are two deep grooves parallel to the profile of the knobs. There are also two more regular parallel grooves near the posterior concave border. They all extend to the tip. In addition, there are a number of small grooves at the proximal end which peter out in the region of the upper end of the flange. On the lateral surface there are some broad, but less marked, grooves. As in most of the other specimens (except that from Tierfontein) the edges of the grooves are irregular and heaped-up in parts.

The fragment, in general, is very similar to the corresponding portion of the Tierfontein horn-core (C 431). The curvature and rotation are rather poorly expressed. The region above knob 3 is almost straight.

Length along anterior (convex) border	700+
Length along posterior (concave) border	430+

	Circumference	*A—P*	*Breadth**
At base	360	138	—
Middle of flange	360	146	77
At knob 2	380	155	73
Just under knob 3	310	122	70
At knob 3	360	141	68
100 mm. above knob 3	250	89	67
At tip	150	52	43

(*Side-to-side.)

TABLE 18. Measurements of 3·53 (mm.).

Old. 1952 *SHK II BK II base* (*S*) and **M 14954b** *Oldy. BK II S.* (Plate 3(*c*), (*d*))

These are two closely fitting fragments belonging to the same left horn-core. M 14954b noted by Hopwood (1936), but he did not include the 'b'.

The flange exhibits a small knob 1 at its centre along the anterior border. Beyond knob 2 (at the upper end of the flange) are knobs 3, 4, 5 and 6.

Distances between the knobs (*mm.*)

1 — 2:	83
2 — 3:	143
3 — 4:	140
4 — 5:	111
5 — 6:	82
6 — tip:	174

There are a number of nutrient foramina (as in 1.53 and 2.53) which are not very large (2–3 mm. in diameter) and not specifically related to the grooves.

It exhibits the same type of curvature and torsion as 1.53 and 2.53 but they are much more twisted and curved. In turn, it shows more torsion than Old. 86 and 3.53. Thus it occupies an intermediate position and this series indicates a further grade of variation of the torsion of the Sivatherine horns.

As in 1.53 and 2.53, there is a medio-posterior knob ('P') on the inferior portion near the base and opposite the flange.

The grooves on the antero-medial surface are large, similar to those in the Hopefield specimens.

The base contains a few sinuses and is hollowed out to a depth of 80 mm.

The horn closely resembles M 14955 (*vide infra*).

Length along anterior (convex) border	840
Length along posterior (concave) border	580

	Circumference	*A—P*	*Breadth**
At base	330	117	100
Flange (knob 2)	350	143	78
At knob 3	360	141	66
Just under knob 4	270	102	—
At knob 4	290	112	62
Just under knob 5	240	90	—
At knob 5	260	94	64
Just under knob 6	220	80	—
At knob 6	240	85	59
Tip	150	49	46

(*Side-to-side.)

Table 19. Measurements of M 14954 (mm.).

M 17027 *Oldy. BK II S.*

The tip and distal portion of a right horn-core. The only interesting features are that the extreme tip is somewhat recurved posteriorly and that the grooves on the antero-medial surface have extended to the base of this recurved portion where they end abruptly. The extreme tip is rather rough and irregularly rounded.

Measurements of M 17027 (*mm.*)

Length of fragment	164		
	Circumference	*A—P*	*Breadth**
Broken end	180	63	59
Tip	—	36	36

(* Side-to-side.)

M 17028

A fragment of bone. It is difficult to be certain whether it is of a horn-core or not. The inner, smooth surface may represent a portion of the endocranial occipital region.

M. 17029 *Oldy. BK II S.*

This is the anterior border of the flange with two knobs. There is also a smaller knob (P) opposite the flange. A fairly deep groove is visible near the knobs.

Measurements of M 17029 (*mm.*)

Distance between knobs 1–2	95
Total length of fragment	228
Breadth of flange (side-to-side)	51

M. 14955 (housed in the British Museum (Natural History) (plate 3(*a*), (*b*))

This is a left horn-core, the knobs pointing antero-laterally and the grooves being on the antero-medial surface. Part of the base is broken away, so that the central (hollowed) part formed by the cranial sinuses is not distinguishable. The posterior portion of the base is rounded, while the anterior flange portion narrows to a ridge. Just above the lower end of the horn-core there is a broad flattened flange, the upper portion of which is broken away in a V-shaped notch just below a knob-like projection on the antero-lateral border. This flange has an S-shaped, curved anterior border which arches forwards, upwards and laterally; then upwards, medially and forwards; and then upwards, medially and backwards. The antero-lateral border of the horn also has two other knobs, and there is a small rough projection just above the highest knob. Just above knob 2 the horn becomes more circular and tends to narrow (A–P) rapidly. The tip of the horn is broken off; but it appears to have pointed horizontally, medially and backwards.

This specimen is noted by Hopwood (1936).

There are deep grooves on the antero-medial surface, which sweep up from the base more or less parallel to the anterior and posterior borders. On the postero-medial surface of the horn-core there are less marked grooves present, some of them being along the axis of the horn, while others are transverse.

Length along the posterior border	560
A–P length across the broadest part of the flange	190
A–P length at the highest part of the flange (knob 2)	165
Breadth (side-to-side) at highest part of flange (knob 2)	85
A–P length at knob 3	117
Breadth (side-to-side) at knob 3	54
A–P at knob 4	88
Breadth (side-to-side) at knob 4	53
A–P at distal extremity of the horn	46
Breadth (side-to-side) at distal extremity of the horn	40

Table 20. Measurements of M 14955 (mm.).

B. Fragments of Jaws

F 3655 *Oldoway II: in situ* 1941, *with others marked 'A'* (plate 4)

It consists of a large fragment of a right maxilla, a portion of the right palatine bone also being intact. It contains M^3, M^2 and M^1. The teeth are in a very worn state; M^1 in particular has been worn almost to the crown-root junction on its anterior pillar.

Buccal surface. The cingulum is rather marked especially in M^3. In M^2, however, the buccal surface is almost completely broken away. Continuous with the rounded cingulum in M^3 and M^2 is a very prominent parastyle, a mesostyle and a metastyle, the parastyle being particularly large and the metastyle being rather rounded. The metastyle of M^2 is almost absent, being heavily impacted against the anterior pillar of M^3, and the enamel in that region is also worn away. The prominence of these styles is most marked on the third molar.

Lingual surface. Rather coarse rugosity. On each tooth there is a cingulum below which there is a slight bulge.

Occlusal surface. The central pits of M^3 and M^2 are U-shaped, although the enamel on the buccal aspect of the pit tends to be rather V-shaped. In M^3 the enamel of the central pit of the posterior pillar is irregular on the lingual side. In M^2, where there is more wear, the limbs of the pits which sweep towards the styles are more or less obliterated; and this is even more obvious in M^1 where the central pit is completely obliterated in the anterior pillar, while the posterior pillar has a small irregular island of enamel remaining, representing the central pit.

On the posterior surface of the posterior pillar of M^3, there is a sharp indentation of the enamel which is also reflected on the root. The posterior buccal root of M^3 is massive and triangular. The buccal roots of the teeth can be seen as the bone is broken away over them, while only the base of the lingual root can be seen, and there are no significant differences in appearances between these and the usual giraffid pattern (*vide supra*).

6 *Old. BK II* (plate 7).

The body of a right mandible, containing M_3–P_2. The vertical axes of M_3 and M_2 are tilted forwards. The enamel of all the teeth is fairly rugose (except for P_2).

M_3 has a rounded cingulum. The rugosity cannot be determined as the enamel is covered by a thin layer of breccia. There is a rudimentary ectostylid and protostylid similar to those of Old. 1 (*vide infra*). The talonid is slightly angulated to the A–P axis of the pillars in a buccal direction.

M_2, M_1 and P_4 have features similar to those of M_3.

P_3 is similar to P_3 of specimen 365 (*vide infra*), except that the paraconid is more separated from the parastylid by a 'pinching in' of the enamel.

P_2

Buccal surface. Finely rugose. There is a rounded cingulum.

Lingual surface. There is a slight cingulum. The parastylid and the metastylid are present.

Occlusal surface. The tooth-shape is triangular. The buccal surface is slightly rounded and the apex of the tooth points anteriorly. The posterior surface of the tooth is markedly worn away.

Wear. The teeth are in advanced wear. On the anterior surface of M_3, the enamel is thinned by 'impaction' of the posterior surface of M_2. On the anterior surface of M_2 the enamel is almost completely worn away; a similar thinning is seen on the contiguous surfaces of M_1 and P_4 where the enamel is completely absent. The contiguous surfaces of P_4 and P_3 show loss of enamel, as does the posterior surface of P_2, but the anterior surface of P_3 has its enamel only slightly thinned. Maximum wear on the premolar is found on the posterior occlusal surface on the buccal side.

Roots. Those of P_2 are broken away on the buccal side, but there are two roots rounded in shape and they are continuous with each other on the area visible above the alveolus, which is about 10 mm.

F 3656 *Oldoway* 1941, *S II* (plates 5(*b*), (*d*); 6(*a*))

A portion of a fragmented left mandible, containing M_3, M_2 and a part of M_1.

M_3

Buccal surface. There is a cingulum on the posterior pillar and talonid, but on the anterior pillar there is a slight depression in the cingulum region and there is an unusual ridge of enamel a few millimetres above the crown-root junction. The rugosity is coarse. The tooth is in a rather advanced stage of wear.

Lingual surface. Rather rugose. Marked cingulum formation. On the posterior surface of the talonid the 'abnormal cingulum' arrangement is also present. Leading up from the cingulum there is a slight entostylid and a slightly more marked parastylid, while the metastylid cannot be detected. The median costa of the entoconid is more obvious than that of the metaconid. The talonid is rounded and its axis is deviated buccally at an angle of about 40° to the A–P axis of the two pillars.

Occlusal surface. The two sides of the central pit of the anterior pillar are in close contact, except anteriorly where they are separated by a small triangular space. The sides of the central pit of the posterior pillar are slightly more separated than in the anterior pillar, and there is a protrusion of enamel in the direction of the talonid. The anterior pillar is more rounded than the posterior pillar, the peripheral enamel of the posterior pillar being more V-shaped than that of the anterior pillar, which is rather U-shaped. Enamel of the anterior surface, where in contact with the posterior pillar of M_2, is almost completely worn away.

M_2

Buccal surface. There is a cingulum with a rounded bulge above it. Coarse rugosity. Its characteristics are generally similar to those of M_3. The posterior surface of M_2 is worn away where it meets M_3, and the anterior surface where it meets M_1 is very worn, as is the posterior surface of M_1, at least half of the surface of which has no enamel whatsoever.

M_1. A part of the anterior pillar is missing.

1 *Old. BK II* (plate 6(*c*), (*d*), (*e*))

This specimen consists of a portion of the body of a right mandible containing M_3–P_4 in a fairly advanced stage of wear.

M_3

Buccal surface. The enamel is coarsely rugose. There is a rounded cingulum which is particularly marked on the anterior pillar and the talonid. There is a very large ectostylid; and there is a slight bulge above the cingulum of the anterior pillar, but the posterior pillar does not show this and near the occlusal surface of both there is a slight concavity of the enamel surface.

Lingual surface. The enamel is coarsely rugose. The cingulum is present, forming a rounded bulge in the region of the base of the entoconid. The features are similar to M_3 of Old. 6. The lingual surface is cracked and the whole crown has been forced lingually.

Occlusal surface. No additional features, except that the enamel is very thick.

M_2. On the buccal surface the features are similar to those of M_3. On the lingual surface the enamel of the posterior pillar is broken away. The appearance otherwise is similar to that of any M_2 described here.

M_1

Buccal surface. There is a great similarity to M_2, except that the bulge above the cingulum is more rounded. A distinct nodular ectostylid is present. The other aspects of the tooth are similar to those of any M_1 described here.

P_4. The general description is identical to that of P_4 of specimen 365.

365 *Old. SHK II*, 1953 (plate 8)

Fragment of a right mandible containing M_1, P_4 and P_3. The teeth are in a very advanced stage of wear.

M_1

Buccal surface. The enamel is rather rugose, and the cingulum is present. On the posterior surface of M_1 all the enamel has been worn away, the contact surface with M_2 being formed by dentine, which itself has been worn away, forming a notch in this surface.

Lingual surface. The enamel has a rather rugose appearance. There is a small cingulum present. No features can be identified because of the marked wear and fragmentation.

Occlusal surface. The central pits are completely worn away, except for a small island of enamel in the posterior pillar. The buccal enamel of the posterior pillar is U-shaped, while that of the anterior pillar is V-shaped.

P_4

Buccal surface. Rather rugose enamel. A cingulum is present, being particularly marked on the hypoconid. A small ectostylid is present between the hypoconid and the protoconid.

Lingual surface. Rather rugose. Cingulum present. The base of the entostylid can be seen. There is a rounded bulge forming the base of the metaconid. The enamel of the posterior surface is worn thin, while that of the anterior surface is worn away completely.

Occlusal surface. The central pit of the anterior pillar is V-shaped, while between the anterior and the posterior pillars there is a small triangular pit. The buccal enamel of the anterior pillar is convex and wide, 'boat-shaped', while the buccal enamel of the posterior pillar is typically in the form of a 'U' compressed from front to back.

Roots. On the lingual aspect, the bases of the roots can be seen. Thus two triangular roots are visible, the anterior being slightly larger than the posterior and they are separated by an inverted V-shaped interval.

P_3

Buccal surface. Coarsely rugose. The cingulum is present, being particularly rounded in the region of the hypoconid.

Lingual surface. Rather rugose. There is a marked rounded cingulum, being particularly marked at the base of the entostylid and not quite as marked at the base of the parastylid. There is a distinct bulge in the region leading up to the metaconid.

Occlusal surface. The whole tooth gives the appearance of an irregular triangle, the buccal surface being more convex than the lingual surface, the apex pointing anteriorly. The posterior surface has its enamel worn away completely, and the dentine has been hollowed out by P_4. The posterior 'pillar' has an irregularly shaped triangular central pit, while all that remains of the central pit of the anterior 'pillar' is a small circular island of enamel surrounding a small pit at the posterior end.

Roots. The root of the anterior 'pillar' has a broad triangular base. It is larger than the root of the posterior 'pillar' which is separated from it by an interval shaped like an inverted V.

Mandible. Because it is highly fragmented and almost completely filled with plaster, it is considered advisable not to take any measurements of the mandible.

392 *Oldoway SHK II E*, 1953 (plate 9)

Fragment of a right mandible containing M_2 and the sockets of M_3 and M_1.

M_2. In an advanced stage of wear.

Buccal surface. The enamel is rather rugose. The cingulum is present, and there is a rounded bulge above it.

Lingual surface. Rugosity is not clear because the tooth is worn smooth on this surface. The cingulum is present. The entostylid and parastylid are present and are continuous with the cingulum at their bases. A metastylid is not present.

Occlusal surface. The lips of the central pit are more widely separated in the posterior pillar than in the anterior.

Roots. The shallow sockets indicate that the roots were short.

3 *Old. BK II* (plate 10)

Fragment of a right mandible with M_3. The tooth is in a fairly advanced stage of wear.

Buccal surface. There is a marked rounded cingulum. Enamel rather rugose. Hypoconulid and ectostylid are present as small nodules. The enamel of the anterior surface of the tooth is broken off, as also the enamel of the lingual surface of the anterior and posterior pillars. The talonid is rather rounded and its axis is in direct line with the longitudinal axis of the anterior and posterior pillars. There is quite a marked V-shaped groove between the enamel surface of the pillars, and also between the posterior pillar and the talonid.

Lingual surface. The enamel of the talonid is rather rugose, and if the talonid is looked at from the posterior aspect the enamel can be seen to bulge and drape down on the buccal aspect in the typical 'apron' effect. The lingual surface of the talonid slopes rather markedly buccalwards and upwards towards the apex from the bulge above the cingulum. The buccal surface has a concavity just above the rounded cingulum.

Occlusal surface. The central pit of the anterior pillar is irregularly U-shaped and closed, while the central pit of the posterior pillar is closed off anteriorly by the enamel of the posterior surface of the anterior pillar, and posteriorly the pit is open and continuous with the central pit of the talonid.

Mandible. Breadth opposite talonid: *c.* 42 mm.

93 *Old. BK II*, 1952 (plates 5(*a*), (*c*); 6(*b*))

Portion of the left mandible, containing M_3 and M_2 and a piece of M_1. The teeth are in a most advanced stage of wear, and the wear is extremely irregular in that the lingual cones of the pillars of M_3 and M_2 have been completely worn down beyond the crown-root junction, while on the buccal aspect a fair amount of enamel is still present. Because this type of wear is the reverse of the usual, it is probable that the cause is a pathological one.

M_3

Buccal surface. The enamel is rather rugose, although it is worn smooth in parts. There is a bulge above the cingulum on the pillars and on the talonid.

Lingual surface. Only the enamel of the talonid and that part where it communicates with the posterior pillar is visible. The talonid is placed at a peculiar angle to the rest of the tooth. Not only is its A–P axis angulated buccally in relation to the mesio-distal axis of the anterior and posterior pillars, but it is also tilted upwards so that its occlusal plane is angulated at 20° to the occlusal plane of the pillars.

Occlusal surface. The central pits of the anterior and posterior pillars are still visible.

M_2

Buccal surface. The buccal portion of the posterior pillar and the roots are broken away, and the surface of the anterior pillar has a rather rugose appearance and a small cingulum.

Lingual surface. The shape of the tooth has been completely disfigured by the abnormal mode of wear, as in the case of M_3.

Occlusal surface. There is a small island of enamel projecting above the surface in the region of the parastylid.

M_1. A portion of the buccal surface of the posterior pillar remains, this pillar being in extreme wear. The rest of the tooth is fragmented and broken away.

92 *Oldoway*, 1952, *BK II* (plate 11)

A fragment of a left mandible, containing M_3 and M_2 and a piece of the posterior root of M_1. The teeth are in early wear and the crown-root junction has not yet appeared above the alveolar surface.

M_3

Buccal surface. This surface is coarsely rugose. The median part of the hypoconid and of the paraconid is rather angulated, especially near the occlusal surface.

Lingual surface. A portion of the mandible is broken away uncovering the crown-root junction where a cingulum can be seen. Just above it there is a bulge, and leading up from the cingulum on the anterior pillar there is a marked narrow parastylid, which does not quite reach the occlusal surface of the tooth. About half-way up from the crown-root junction, the base of the metastylid commences and near the occlusal surface it becomes a prominent ridge overlapping the anterior portion of the entoconid. The median ridge of the metaconid is prominent for about the same distance as the metastylid. The median ridge of the entoconid is prominent, but the entostylid is much less marked. The lower $\frac{2}{3}$ of the lingual surface of the enamel of the anterior and posterior pillars are fused in the region of the metastylid, but the upper $\frac{1}{3}$ is separated by a groove. This surface of the entostylid is continuous with that of the talonid.

Occlusal surface. The tooth is in early wear which is most marked along the anterior portion of the protoconid. The central pits are V-shaped, their hollowed portions being continuous with each other in the region between the two pillars, while the central pit of the posterior pillar is continuous with a small central pit of the talonid. The central pit of the anterior pillar is closed off anteriorly where the enamel of the paraconid fuses with that of the protoconid.

M_2. The general characters of M_2 are similar to those of M_3, except that the entostylid and parastylid are more marked than in M_3, and the metastylid presents a vertical groove which kinks it posteriorly.

91 *Old. BK II*, 1952

This specimen consists of the posterior portion of the left body of a mandible including the angle, and contains M_2, a part of M_1, and the roots of M_3. Owing to previous inaccurate reconstruction M_1 appears to be lower than M_2.

M_2

Buccal surface. Coarsely rugose. Cingulum present. The enamel is thickened above the cingulum of the posterior pillar. A small ectostylid is present. The tooth is in a medium stage of wear.

Lingual surface. Finely rugose; cingulum present. It has the general characters of M_2 described previously. A portion of the metaconid is absent.

Occlusal surface. Shows two central pits; their lips are fairly widely separated, the anterior pit broadening out anteriorly and the posterior pit broadening out posteriorly. The enamel of the anterior surface of the anterior pillar is worn rather thin due to contact pressure of M_1.

M_1. The general description is similar to that of M_2, but it is markedly impacted against M_2, so that its entostylid appears rather squashed.

Oldoway BK II—East Nguntiri site, 1953 (plate 12)

Fragment of an unnumbered left mandible containing M_1, M_2 and the anterior pillar of M_3. It is in an advanced stage of wear.

M_3

Buccal surface. There is a small rounded cingulum above which the buccal surface is flat. Fairly rugose.

Lingual surface. The enamel is chipped away.

Occlusal surface. The anterior pillar has a rounded appearance. The parastylid is small.

M_2

Buccal surface. Rounded cingulum above which the enamel bulges fairly markedly forming a ridge. Fairly rugose enamel.

Lingual surface. It has the general characters of other M_2 described previously.

Occlusal surface. The central pits of M_2 are linear. The posterior pit has an extension up towards the entostylid.

M_1. Rather similar in general appearance to M_2.

321 *Old. BK II Ex.* 1953 (plate 13)

Fragment of a left mandible containing a portion of an anterior pillar of M_3 and a fragmented M_2. It is at the same stage of wear as the Nguntiri specimen.

M_3. The buccal surface of the anterior pillar is rather flattened out and rounded. It has a finely rugose enamel.

M_2. It is in rather advanced wear.

Buccal surface. There is a small cingulum which has a small rounded bulge above it on the anterior pillar. Finely rugose enamel. The anterior surface of the anterior pillar is broken away.

Lingual surface. Fairly rugose. Cingulum present leading up to reach the parastylid and entostylid. The parastylid is prominent.

Occlusal surface. It presents an identical appearance to any other molar at a similar stage of wear. The enamel of the posterior surface of the posterior pillar is slightly thinned out due to contact wear by M_3.

C. Isolated Teeth

F 2989 *Oldoway,* 1941, *II, in situ with 'A'* (plates 15(*e*); 16(*e*); 17(*e*))

This is an isolated upper left premolar, probably P^3 (*vide infra*), in an extremely advanced stage of wear which is reminiscent of that of M^1 of F 3655. The lingual surface is completely worn away, while the buccal surface presents a fairly rugose enamel. Just as the wear is more marked on the lingual surface, so it is more marked on the anterior surface. The base of a rather large and rounded metastyle is present.

Occlusal surface. Only a small slit remains of the central pit, as well as a small island of enamel near the metastyle.

Roots. The lingual root, which is broken off near its tip, is enormous with a rather convex lingual surface and a flattened buccal surface. There are two buccal roots, the anterior one being oval, the posterior one being triangular. The anterior root is broken off near its tip.

The measurement of the mesio-distal length of the root, just above the crown-root junction is 27·1 mm. which compares favourably with the length of the root of the Hopefield P^3 (4025), viz. 29·7 mm.

Determination of the diagnosis of F 2989

In order to determine which upper premolar it is, the premolar index (see Section I) has been calculated.

Morphologically, specimen F 2989 seems to belong to the same individual maxilla as F 3655. Both were found in 1941, 'with A', and they look very much the same, i.e. degree of wear, type of fossilization, colour of tooth and breccia.

The premolar index for the transverse breadth is $\frac{P?}{M^1} = \frac{43}{47} = 91{\cdot}48$.

In *G. camelopardalis*, the same premolar index for the transverse breadth is

	N	M. & s.e.	σ	V	Range of Variation
$\frac{P^3}{M^1}$	108	91·03±·469	4·84	5·31	73·6—106·2
$\frac{P^4}{M^1}$	108	95·74±·458	4·72	4·93	83·0—109·5

According to these figures, the premolar index of F 2989 is more closely related to that of P^3/M^1 than to that of P^4/M^1, and it should rather be considered as a P^3.

However, it should be noted that 91·48 is different from the mean value of P^4/M^1 by less than one sigma (95·74—4·72 = 91·02) so that no conclusive significance could be attached to this mathematical approach of the problem of determination, especially in view of the large range of variation.

F 2993 *Oldoway II, with 'A'* (plate 14(*a*), (*b*), (*c*))

Isolated upper right molar, probably M^2. It is in a fairly advanced stage of wear, and has a rather rugose enamel, and a cingulum which is very marked on the anterior pillar. There is a small entostyle and hypostyle.

Buccal surface. The paracone is missing, but the metacone shows the usual characters except that the cingulum is a very marked ridge, and that the central costa of the metacone is not quite confluent with the cingulum at its base. There is a heaped-up ridge of enamel just above the cingulum.

Lingual surface. Below the rolled lower edge of the cingulum, the enamel appears to be thrown into folds.

Occlusal surface. It is typical of the upper molars with no unusual features, except that the enamel surface of the hypocone is quite widely separated from that of the protocone where they tend to come together between the two pillars.

4 *BK II* (plates 15(*b*); 16; 17)

Isolated right M^3, with the metacone broken away. It is in a most advanced stage of wear.

Buccal surface. There is a marked cingulum. The typical formation of the styles are seen here again, but the ridge of enamel leading to the paracone is not very marked.

Lingual surface. The enamel is fairly rugose, but is thrown into ridges forming an entostyle and a small protostyle. There is a cingulum and the tooth bulges below it. Here, as in all other M^3, the posterior pillar projects less in a lingual direction than does the anterior (cf. Hopefield 4024, Old. 3655). In all other upper molars the posterior pillar projects more lingually.

There is a typical marked angulation of the lingual surface from the base towards the apex in a buccal direction.

Occlusal surface. The central pits are most irregular on the lingual side, the buccal enamel lip being V-shaped, while the lingual enamel is irregularly U-shaped. The pits of the two pillars are in continuity in the region of the mesostyle.

Roots. Typical formation of the lingual root with its more massive anterior portion formed by a vertical depression between the anterior and the posterior portions of the lingual aspect. The buccal roots are roughly triangular in shape, the posterior one being larger, and its tip curves posteriorly.

109 *Olduvai BK II* (1955) (plate 14(*d*), (*e*), (*f*))

Isolated upper left M^3 in early wear, with a portion of the hypocone broken off. The enamel is finely rugose. There is a cingulum present and a very small entostyle, while a ridge of enamel represents both the hypostyle and the protostyle. There is a slight bulge below the cingulum and the lingual surface slopes at a marked angle towards the apex in a buccal direction.

Buccal surface. The cingulum and its styles are typical of the teeth described previously, except that the styles are not as obvious as, for example, in F 3655.

Occlusal surface. The central pits are in continuity with each other. The paracone is rather widely separated from the protocone, but the metacone is closer to the hypocone, and in fact the apex of the metacone tends to be twisted in a lingual direction.

Roots. The roots are broken off at the base.

F 2992 *Olduvai II, in situ with 'A'*

This is an isolated upper molar in a very fragmented state. It is not possible to determine which molar it is and to which side it belongs. It shows characteristics similar to analagous portions of upper molars previously described. It is in a fairly advanced stage of wear.

97 *Old. BK II,* 1952

Isolated right canine with the mesial portion of its enamel broken away. The tooth is in an advanced stage of wear.

Buccal surface. Marked cingulum with a rounded bulge above it. The enamel is coarsely rugose. The tooth is partially bilobed, the outer lobe projecting beyond the true transverse plane of the longest axis of the root.

Lingual surface. The dentine is hollowed out laterally. The occlusal edge shows a broad rim of wear. The occlusal edge of the tooth slopes outwards and backwards.

Crown height	*c.* 32 mm.	Maximum breadth	15·0 mm.
Length	28+ mm.	Tooth height	*c.* 60 mm.

F 2991 *Old. I S*, 1941 (plates 18(*a*); 19(*a*); 20(*a*))

Isolated right P_4, in a fairly advanced stage of wear.

Buccal surface. Coarsely rugose; marked cingulum especially at the base of the hypoconid. A nodular ectostylid is visible.

Lingual surface. There is a cingulum. Rugosity is coarse, although the tooth is worn smooth over the major part. The parastylid and the metastylid are prominent, the parastylid rising up as a distinct ridge from the cingulum. The median ridge of the metaconid is present.

Occlusal surface. The central pit of the anterior pillar is rather wide anteriorly; it narrows in the centre, and then forms an open slit between the metastylid and the entoconid. The posterior pillar has a central pit which has a rounded formation anteriorly and which narrows posteriorly in the region of the entostylid.

Roots. They are broken off near the base, the posterior root appearing large and quadrangular-shaped, the smaller anterior root being somewhat oval with a concavity on its posterior aspect. On viewing the posterior aspect, the 'apron' effect of the enamel is visible.

2 *Old. BK II* (plates 15(*a*); 16; 17)

Isolated right P_4. It has the general characteristics of F 2991, although it is in a slightly less advanced stage of wear. The roots have been repaired and replaced at an abnormal angle.

5 *Old. BK II* (plates 15(*d*); 16; 17)

Isolated left P_4, with the roots broken away. The tooth has just commenced wear.

Buccal surface. It shows a coarse rugosity and a cingulum which is particularly accentuated at the base of the hypoconid. An ectostylid is present on the posterior part of the protoconid.

Lingual surface. Cingulum present. The entoconid shows a marked bulge about half-way up the posterior aspect of the tooth. The median ridge of the metaconid is prominent and there is a distinct metastylid which overlaps the lingual surface of the entoconid and is separated from it by a wide interval near the occlusal surface, but is fused with it near the base of the crown.

Occlusal surface. Two wide central pits are present. The hypoconid is separated from the protoconid by a wide V-shaped interval in the upper $\frac{2}{3}$ of the tooth, but is fused with it in the lower $\frac{1}{3}$ (as in F 2991 and 4).

7 *Old. BK II*

Isolated right P_4. The roots are absent. Part of the base of the anterior pillar is missing, and part of the lingual surface is absent.

Buccal surface. Coarsely rugose, and there is a thick cingulum at the base of the posterior pillar. Very similar to 5, except that the hypoconid is not separated from the protoconid by a wide interval, but only by a furrow, and that the ectostylid appears here only as a minute nodule. The tooth has just erupted and is not in wear at all.

96 *Old. BK II*, 1952

Isolated left P_4, with a part of the buccal surface, the base and the roots missing.

Lingual surface. Very similar to that of F 2991.

Occlusal surface. Is also similar to F 2991 except that the central pit of the anterior pillar is now closed off and there is a small island of enamel near the parastylid, and the enamel of the entostylid has fused with that of the metastylid.

105 *Old. BK II ex.* 1953 (plates 18(*c*); 19(*c*); 20(*c*))

Isolated right M_1. Part of the anterior root is broken off and a portion of the buccal enamel of the posterior pillar is chipped off.

Buccal surface. A small cingulum is present. The enamel is thickened in the region of the ectostylid. The hypoconulid is formed by a marked vertical ridge, although it is worn away at its base. The enamel is rather rugose.

Lingual surface. Small cingulum. It leads up to a parastylid on the anterior pillar, and on the posterior pillar the entostylid seems to have a rather broad base, and it is separated from the median ridge of the entoconid by a slight vertical furrow. The base of the mesostylid can be identified and it is continuous with the metaconid.

Occlusal surface. The pillars have a rather circular shape. The central pits are slightly curved with their convexities facing buccalwards, the anterior portion of the anterior pit being larger than the posterior portion, while the posterior part of the posterior pit is triangular and its lips are more widely separated than those of the anterior portion of the pit. The buccal enamel of the central pit of the anterior pillar is continuous with the lingual enamel on the entoconid. There is a slight kinking of the enamel in the region of the metastylid.

Roots. The posterior root is broad and curves posteriorly at its tip in an abnormal fashion and on its posterior surface it has a prominent ridge which appears to be continuous with the unusually large hypoconulid. On the posterior aspect of the base of the anterior root there is an aberrant root nodule which has been broken off.

132 *Old. BK II*, 1953

Isolated right M_1, in a very advanced stage of wear. Both roots are broken off at the base.

Buccal surface. Rather rugose. Very slight cingulum. The crown is rounded just above the cingulum. A small ectostylid is present. The anterior surface of the tooth has a piece missing.

Lingual surface. The posterior pillar has almost all its enamel worn down by abnormal wear (cf. specimen 93). The cingulum is barely recognizable on the anterior pillar. The enamel is rather rugose. The base of the central ridge of the metaconid is just recognizable where it fuses with the metastylid.

Occlusal surface. The central pits are irregular in shape. The central pit of the anterior pillar presents a bow-tie effect. The posterior surface has its enamel worn away completely.

95 *Old. BK II,* 1952 (plates 18(*b*), 19(*d*); 20(*d*))

A right M_2. The roots are broken off at the base.

Buccal surface. There is a fairly well-defined cingulum on the anterior pillar which is less marked on the posterior pillar, and a prominent protostylid leads up from the cingulum. There is a small nodular ectostylid prolonged on to the posterior pillar while there is an elevated ridge (hypostylid) on the posterior aspect of the pillar. There is a small hypoconulid present. The enamel is rather rugose.

Lingual surface. There is a small cingulum. The parastylid is broken off and the median ridge of the metaconid is prominent and rounded and is hardly separated from the metastylid, so that the general impression of the anterior pillar is that there is a very broad convex portion on the lingual surface (cf. Old. 120, *infra*). On the posterior pillar, the entostylid is a small narrow ridge and hardly separable from the entoconid. Seen from the anterior or the posterior aspect, the buccal enamel presents the 'apron' effect.

Occlusal surface. The central pit of the anterior pillar is broad anteriorly, while posteriorly it tends to slope towards the metastylid and in the central portion the two enamel surfaces almost approximate each other. The central pit of the posterior pillar presents a U-shaped appearance of the buccal lip of enamel, and a V-shaped one of the lingual lip.

120 *Old. BK II,* 1955 (plates 18(*e*); 19(*e*); 20(*e*))

Isolated left M_3, with most of the roots missing. It has a rolled appearance and is in an advanced stage of wear.

Buccal surface. The pillars have a marked cingulum; on the anterior portion of the posterior pillar, the cingulum is less marked, while it is most marked on the talonid. A short ectostylid is present. The surface is rather rugose. The buccal surface slopes quite markedly towards the apex in a lingual direction. There is no or very slight rounding above the cingulum. A slight cingulum is present on the anterior surface of the anterior pillar.

Lingual surface. Cingulum is marked on the pillars, but least marked on the talonid. Leading up from the cingulum of the anterior pillar, there is a rather marked parastylid; the metastylid is absent, and there is only a minute entostylid. However, the central ridge of the metaconid is extremely broad and rounded while the central ridge of the entoconid is also very large, but it is smaller than the metaconid. Between the entoconid and the metaconid the enamel folds rather deeply in a buccal direction emphasizing the metaconid and the entoconid even more. The metastylid has fused with the metaconid and thus produces this large bulge, and similarly part of the entostylid has probably joined the entoconid to produce the latter's large size (cf. specimen 95). The talonid is rather large and rounded; a hypoconulid is present. The buccal enamel of the posterior pillar is continuous with that of the anterior pillar but the two pillars are rather separated, which is a general variable feature of the lower molars.

Occlusal surface. The central pit of the anterior pillar is shaped like a bow-tie, in that the anterior portion is triangular in shape, and the central pit is still obvious, as also the posterior portion, but in between the two enamel lips are lying against each other. In the posterior pillar, the central pit has a similar appearance except that the anterior portion is more oval, the posterior portion is narrower and is continuous with the central pit of the talonid, which is fairly large. The enamel is generally very thick in this tooth.

Marsabit Road (plate 14(*g*), (*h*), (*i*))

This specimen has no number. It is a left third lower molar. Part of the talonid is broken off, as well as a part of the anterior surface.

Buccal surface. The pillars have a marked cingulum and it is coarsely rugose.

Lingual surface. Idem. The tooth is in advanced wear. The ridge of the parastylid can just be made out, while the metastylid has fused with the metaconid.

Occlusal surface. The anterior central pit is L-shaped. The posterior central pit is broadly U-shaped, and just behind it there is a rather wide central pit on the talonid. Although the roots are broken, they appear to be very short.

166 *Old. BK II*, 1955 (plates 18(*d*); 19(*b*); 20(*b*))

Isolated right lower molar, probably M_2, in early wear.

Buccal surface. It has a distinct rounded cingulum, more prominent on the anterior pillar than on the posterior one. The enamel shows a coarse rugosity. The ectostylid is represented by a small ridge of enamel. There is a small parastylid and a protostylid present. No hypoconulid. The metastylid is very prominent.

Lingual surface. A well demarcated cingulum leads up to a marked parastylid and a slightly less marked entostylid which however is broken off near the occlusal surface. The central ridge of the metaconid is well defined, and is separated from the metastylid by a slight depression. The entoconid is broken off.

Occlusal surface. The central pit of the anterior pillar is slightly curved and is wider anteriorly than posteriorly. The central pit of the posterior pillar appears to be V-shaped: a part of the pit is broken away.

116 *Old. BK II Ex.* 1953 (plates 15(*c*); 16(*c*); 17(*c*)).

Isolated right lower molar, just commencing wear, with the hypoconid missing and a portion of the entoconid broken. The roots are broken. It is probably a M_1.

Buccal surface. The cingulum cannot be observed because the tooth has been broken away. Surface coarsely rugose.

Lingual surface. The parastylid is a marked ridge. The central ridge of the metaconid has a ribbed appearance, and a prominent metastylid is on the upper half of the tooth; the central ridge of the entoconid also has a ribbed appearance.

8 *Old.*

An isolated pillar of a left lower molar in early wear.

Buccal surface. There is a rounded cingulum present. Small ectostylid. Rather rugose.

Lingual surface. Small cingulum leading up to a small ridged parastylid. The central ridge of the metaconid is only obvious near the occlusal surface.

Occlusal surface. The central pit shows an anterior widening and a posterior narrow part, and the central portions of the enamel surfaces are continuous.

100 *Old. II Ex.* 1953

This is an isolated entoconid of a lower right molar. Wear is just commencing. It presents the general features of entoconids previously described.

98 *Old. BK II,* 1952

Broken isolated fragment of the entoconid of a lower right molar.

99 *Old. BK II,* 1952

An isolated fragment of a lingual pillar of an upper molar.

Marsabit Road

This specimen has no number. It is the posterior pillar of a right lower M_3 with a small fragment of its root. It is in advanced wear and has the general characteristics of M_3 specimens previously described, except that its buccal pillar is markedly twisted posteriorly. The central pit is V-shaped and it has an irregular infolding of enamel posteriorly. There is a marked ectostylid present.

The only measurements that can be taken are:

Maximum breadth	*c.* 32 mm.
Occlusal length	24·0 mm.

Oldoway Surface (plates 18(*f*); 19(*f*); 20(*f*))

It is a right lower molar, probably M_1 in an intermediate stage of wear. Most of the posterior pillar and root are absent, and the anterior portion of the anterior pillar is broken away.

Buccal surface. Enamel rugose; cingulum is present and there is a slight bulge above it.

Lingual surface. Fairly rugose, but worn smooth. The parastylid and the metastylid are well defined.

Occlusal surface. Central pit has a typical bow-tie appearance.

Note.—The measurements of all the teeth are given in table 40 at the end of section 2.

D. Postcranial Skeletal Remains

116p *Old. BK II,* 1952 (plate 23(*d*))

The letter 'p' has been added to this number by the authors so as to differentiate it from the dental fragment with the same number (*supra*).

Proximal end of a right ulna. This presents a massive olecranon process which is separated from the articular facets by a massive rectangular 'slab' of bone. The shaft of the ulna is broken off.

Olecranon process (posterior extremity) to articular facet along superior border	184 mm.
Olecranon process, maximum height	117 mm.
Olecranon process, maximum side-to-side breadth	78 mm.
Breadth at centre of the 'slab'	30 mm.
Maximum breadth of articular process	94 mm.

Most of its articular surface (i.e. about $\frac{7}{8}$) is for articulation with the humerus; only two small facets below this are for articulation with the radius. The surface area of the radial articulation is relatively less than in the modern giraffe.

115 *Old. BK II,* 1952 (plate 21(*b*))

Distal epiphysis of a right radius presenting a marked inferiorly projecting tuberosity.

Maximum breadth at radial tuberosity	122 mm.
Maximum breadth at proximal end of fragment	135 mm.
Maximum A–P length	82 mm.

341 *Old. BK II,* 1952 (plate 21(*e*))

Os magnum of the left carpus: very similar to that of modern giraffe.

Maximum length A–P	75 mm.
Maximum breadth	70 mm.
Maximum thickness of postero-lateral side	39 mm.

114 *Old. BK II*, 1952 (plate 22(*a*))

Distal end of a metacarpal and a piece of the distal shaft: fragments have been broken off, and the distal end has been chipped and rolled. In comparison with the distal end of the metatarsal (*vide infra*, specimen 314) the shaft presents a definite flattened appearance, convex anteriorly and scooped out posteriorly. It is almost identical in appearance to a specimen described by Dietrich (1937), E 122 from Oldoway (his text-figs. 1 and 2, and table VI, fig. 1), and another from Serengeti (Garussi-Korongo 1.39) also described by Dietrich (1942) (his table XXII, fig. 187). The latter specimen is still a young individual with an epiphysis; specimen 114 from Olduvai has a fused epiphysis and the distal end appears to be broader.

Maximum breadth across condyles	105 mm.
Maximum breadth of lateral condyle, taken anteriorly ..	51 mm.
Maximum breadth of medial condyle, taken anteriorly ..	52 mm.
A–P length of the condyles	54+ mm.
60 mm. above the distal end: A–P of the shaft	42 mm.
Breadth of the shaft	79 mm.

100 *Old. BK II*, 1952 (plate 23(*c*))

Distal extremity of a right femur, consisting of 2 condyles and the patellar condyle.

Maximum breadth across the condyles	161 mm.
Maximum breadth across medial condyle	72 mm.
Maximum breadth across lateral condyle	55 mm.
Maximum breadth across patellar condyle	78 mm.
Cord length of the patellar condyle in the centre	109 mm.

101 *Old. BK II*, 1952 (plate 21(*c*))

Distal end of a left tibia which articulates with numbers 102, 103. Adult. It presents a marked bulge above the medial malleolus and another large rough tuberosity on the antero-lateral aspect just above the articular surface. Leading down from the shaft to this tuberosity there is a large linear ridge.

Distal extremity: Maximum A–P	83 mm.
Maximum breadth	120 mm.
About 80 mm. from distal end: A–P	64 mm.
Breadth	87 mm.

112 *Old. BK II*, 1952

Distal extremity of a right tibia, which is similar in many respects to 101, except that it is smaller.

Distal extremity: Maximum A–P	83 mm.
Maximum breadth	109 mm.

103 *Old. BK II*, 1952 (plates 23(*a*), (*b*); 24(*c*))

Left calcaneum, articulating with 102 and 104. It is a massive bone with a markedly prismatic proximal tuberosity (*tuber calcis*). The body of the bone is broad from front to back, and constricted from side to side. The facet articulating with the posterior surface of the astragalus (talus) is irregular in shape, and has a narrow downward and posterior projection, while it is broad and quadrangular above this. The fibular facet, for articulation with the fibular sesamoid, is quadrangular in shape, convex from front to back and is angulated from behind forwards in a medial direction. At the distal extremity, on the inferior aspect of the lateral side, there is a concave articular facet arched upwards for articulation with the cuboid; it has a lateral convex border, and medially it has a concave border.

108 *Old. BK II*, 1952

A left calcaneum, shorter than 103, presenting roughly the same features, except (1) that the tuberosity is more rounded and massive, (2) that the body is shorter, and (3) that the fibular facet is smaller and more angulated medially.

	103 *mm.*	*108* *mm.*
Maximum length of calcaneum	216	198
Maximum breadth (side-to-side) of tuberosity	69	67
Maximum height (A—P) of tuberosity	69	*c.* 62
Maximum length (A—P) opposite the fibular facet ..	89	91
Body length from the superior border of astragalus facet (along the anterior border)	131	*c.* 119
Minimum body breadth	39	42
Fibular facet: A—P length (on the convex portion) ..	39	33
Breadth	28	24

Table 21

102 *Old. BK II*, 1952

Astragalus (talus), belonging to the left side, articulating with the distal end of the tibia No. 101 proximally, and with No. 104 distally, and with No. 103 posteriorly. The proximo-lateral articular ridge, for articulation with the lateral fossa of the tibia, is large and wide, whereas the medial articular ridge is narrow and has a large articular surface on its medial aspect for the medial malleolus of the tibia. On the lateral aspect of the bone, just behind the mid-point, there is a big oblique quadrangular-shaped surface for the articulation of the calcaneum, and at the anterior end there is a small irregularly rounded facet for articulation with the anterior extremity of the calcaneum. Between these two surfaces there is a rough, hollowed-out region for the interosseous ligament. On the anterior aspect, the fossa for reception of the lower border of the tibia is long and saddle-shaped.

107 *Old. BK II*, 1952 (plate 21(*a*))

Right astragalus, with features similar to those previously described in specimen No. 102. Because of the proximity of their discovery, they probably belong to the same individual. Articulates with No. 110.

	102 mm.	107 mm.
Maximum proximo-distal length	113	112
Maximum A—P diameter, medially ..	73	71
Maximum A—P diameter, laterally ..	64	63
Maximum breadth, proximally	87	86
Maximum breadth, distally	*c.* 75	76
Maximum articular breadth proximally ..	74	73
Maximum articular breadth distally ..	*c.* 75	76

TABLE 22

104 *Old. BK II*, 1952 (plates 21(*d*); 24(*g*))

A left cubonaviculare, articulating proximally with astragalus No. 102 and calcaneum No. 103, distally with cuneiform No. 105 and metatarsal No. 106. Proximally, the medial facet for articulation with the astragalus is much broader than the lateral one, the two being typically separated by a ridge. The tuberosity of the naviculare is short but very broad and massive. Laterally, on the proximal surface, is the bean-shaped facet for articulation with the calcaneum. On the distal surface, the articular facet of the cuboid which articulates with the upper surface of the lateral metapodial is longer and broader than the medial articular facet of the naviculare for the fused cuneiforms. Posteriorly to this facet and continuous with it, there is a small rounded facet for the external cuneiform. Posterior to the cuboid articular facet for the metatarsal, there is a well-defined groove which runs transversely. Posterior to this groove there is a tuberosity which does not have an articular facet for articulation with the metatarsal. This facet is present in the modern giraffe.

109 *Old. BK II*, 1952

Isolated right cubonaviculare. The features are very similar to those described in the previous specimen (104).

110 *Old. BK II*, 1952

Right cubonaviculare, articulating with No. 107, 110 A and 111. It has identical features to No. 104. Probably belongs to the same animal.

	104 mm.	110 mm.	109 mm.
Maximum breadth (side-to-side) across the centre	110	108	101
Maximum A–P length across the tuberosity of naviculare	106	106	95
Maximum length of naviculare articulating facet for cuneiform	55	55	48
Maximum breadth of naviculare articulating facet for cuneiform	37	37	35
Maximum length of cuboid articulating facet for metatarsal	61	61	55
Maximum breadth of cuboid articulating facet for metatarsal	45	48	42

TABLE 23

105 *Old. BK II*, 1952 (plate 21(*g*))

Left cuneiform consisting of the fused I and II cuneiforms. It has an oval shape. It articulates with No. 104 and 106. The proximal surface is concave from front to back. The distal surface is slightly convex in the central portion. Medially and posteriorly there is an irregular prominence, the upper border of which is in the same plane as the articular facet. On the surface of this prominence are a number of almost parallel grooves which run from above in a downward and forward direction: they are probably grooves formed by the astragalo-metatarsal ligament. On the antero-medial part of the superior border, the articular surface has a small lip which projects downwards. It articulates with a similarly shaped small projection on the cubonaviculare, at the junction of the cuboid with naviculare, at the antero-medial part of the opposing facet.

110 A *Old. BK II*, 1952

A right fused cuneiform, articulating with No. 110 and 111. It is identical in appearance to No. 105, but its posterior portion is broken off.

	105	*110 A*
Maximum A–P length	68 mm.	59 mm.
Maximum breadth side-to-side	41 mm.	40 mm.
Maximum thickness (postero-lateral)	23 mm.	23 mm.

106 *Old. BK II*, 1952 (plate 24(*a*), (*b*), (*f*))

This is a proximal end of a left metatarsal and a piece of the shaft. It articulates with Nos. 104, 105. The anterior median groove is extremely wide with marked ridges on each side. Proximally are three articular facets—two are kidney-shaped facets for the cubonaviculare, while in between them and slightly medially and posteriorly is the facet for the small rounded external cuneiform.

111 *Old. BK II*, 1952

Proximal end and portion of the shaft of a right metatarsal, showing similar features to 106. It articulates with Nos. 110, 110 A.

	106 *mm.*	*111* *mm.*
Maximum length (A–P) at proximal end	81	84
Maximum breadth at proximal end	93	95
About 60 mm. below: A–P of shaft	67	65
Breadth	65	72
Maximum A–P of medial articular surface	59	59
Maximum A–P of lateral articular surface	64	58
Maximum breadth across centre of medial articular surface	33	36
Maximum breadth across centre of lateral articular surface	40	*c.* 50

Table 24

314 *Old. BK II, Ex.* 1953 (plate 24(*d*), (*e*))

This is the distal third of a right metatarsal. It presents a deep and wide central groove anteriorly, of which the lateral lip is more prominent and higher than the medial. The anterior surface has a general convex appearance, while the posterior surface is flattened. Posteriorly a shallow and ill-defined groove can be seen centrally, leading down to the space between the trochleae ('Rollen', Dietrich, 1942). On the outer aspect of each trochlea, there is a fossa for the attachment of collateral ligaments, and the lateral one is deeper and larger than the medial. Above the medial fossa there is a rough tuberosity which is larger than the lateral. The trochleae are big and separated by a deep groove; at the base of the groove, where fusion has occurred, there is an extensive central pit extending upwards. The grooves for the sesamoid bones are shallow, the deepest one being the most lateral.

Maximum breadth at the trochleae	109 mm.
Breadth of the lateral trochlea	52 mm.
Breadth of the medial trochlea	53 mm.
A–P length across the trochlea, medially	61 mm.
laterally	63 mm.
Breadth of the distal extremity across the tuberosity	102 mm.
Shaft some 120 mm. above the distal extremity	
maximum breadth	67 mm.
maximum A–P	*c.* 60 mm.

M 14687

This is an articulated hind limb in the British Museum (Nat. Hist.) and Hopwood's paratype (1934). The femur, proximal end of the tibia and the 2nd and 3rd phalanges are missing. The measurements (mm.) are:

Tibia	
Total length	400+
Length: crest of tibia—distal extremity	230
Distal extremity: Maximum A–P	71
Maximum breadth	103
Metatarsal	
Maximum length	411
Proximal extremity: Maximum A–P	81
Maximum breadth	83
Distal extremity: Maximum A–P	54
Maximum breadth	90
Phalanx I	
Maximum length	104
Proximal extremity: Maximum A–P	50
Maximum breadth	48
Distal extremity: Maximum A–P	30
Maximum breadth	40

113 *Old. BK II*, 1952

185 *Old. BK II, Ex.* 1953 (plate 22(*c*))

F 364 *Old. S I*, 1941 (plate 22(*b*))

Old. 'Surface' (plate 22(*d*))

F 3297 *Old. II*, 1941, *with 'A'*

F 365

These are all proximal phalanges and it is not possible to say with any degree of certainty whether a particular phalanx is a medial phalanx of the right limb or whether it belongs to the lateral side of the left limb; or whether a lateral phalanx of the right may belong to the medial side of the left. Furthermore, it is not possible to state whether an individual phalanx belongs to the fore or hind limb; but we have observed that in one particular extant animal the proximal phalanx of the fore limb is more massive than that of the hind limb. On this basis it is suggested that specimen F 3297 and 'Oldoway surface' probably belong to fore limbs, while the other four specimens probably belong to hind limbs.

	185	*113*	*F364*	*Surface*	*F3297*	*F365*
			(*mm.*)			
Maximum length	107	108	113	120	—	114
Breadth (side-to-side) at base ..	50	*c.* 51	44	60	60	52
A–P at base..	54	*c.* 51	48	58	57	51
Minimum breadth, shaft	46	43	37	47	—	39
Distal extremity:						
Maximum breadth (side-to-side)	48	49	46	58	—	48
Maximum A–P length	33	34	29	38	—	31

TABLE 25

342 *Old. BK II*, 1952 (plate 21(*f*))

Sesamoid bone articulating with the head of the middle phalanx and the base of the distal phalanx.

Maximum A–P	53 mm.
Maximum breadth	36 mm.
Maximum thickness	34 mm.

CHAPTER 2

ORANGE FREE STATE (UNION OF SOUTH AFRICA)

A. LOCALITIES

Fossil Sivatheriinae have been recovered from five different localities of the Orange Free State which extend over a large area (the furthermost points being about 150 miles apart), but they all belong to the Vaal River basin (fig. 18). Consequently, in spite of the fact that some of the specimens have been described by different individuals, that they have been found at various stratigraphical levels and that they are housed in different museums, the general geological picture of the Vaal River basin (Cooke, 1949) provides good reason to consider them in one group.

The fossil specimens are recorded as being derived from the following sites:

1. MMK 3685 (McGregor Memorial Museum, Kimberley) is stated as

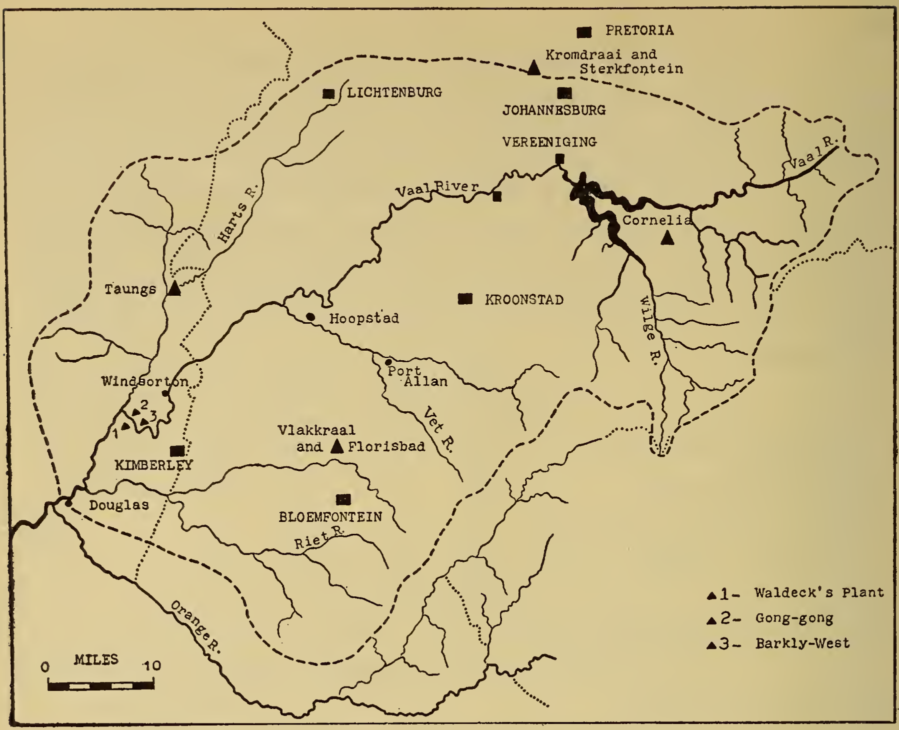

Fig. 18. Map of Vaal River basin indicating major fossil sites (▲) (modified after Cooke, 1949).

coming from an 'unknown locality of the Vaal River basin' (Haughton, 1922). Assigning this tooth to a new genus and species, *Griquatherium cingulatum*, Haughton stated that it came from the collection of Mr. A. Grumpelt at Barkly West, and Cooke (1949) stated that on the basis of the other specimens in this collection, it is quite likely that the *Griquatherium* specimen came from the 60-foot terrace at Waldeck's Plant or Gong-gong.

2. In 1926, three Sivatheriinae teeth were recovered from the upper layers at Florisbad (Dreyer and Lyle, 1931). The actual teeth were sent in 1932 to scientists in Europe for study, but unfortunately they were not described and it is now not possible to trace them. The only remnant of the specimens is a poor plaster-cast of the crown of a lower molar (C 1492) which is housed in the Nasionale Museum, Bloemfontein.

Notes on the geology of Florisbad have been published on various occasions (Dreyer and Lyle, 1931; Dreyer, 1938; Hoffman, 1953; Oakley, 1954a; Singer, 1956, and Meiring, 1956). Oakley (1954a, page 84) states:

'The Florisbad deposits consist of sands, intermittently ejected by springs of gaseous water during Pleistocene and recent times, alternating with seams of peat formed by salt marsh vegetation which spread across the area when the springs were quiescent. There are two parallel lines of spring centres (or "eyes") which have become sealed off progressively in an easterly direction. Thus the "eyes" are fossilized on the western side of the site but still active on the eastern side.

'Fossil mammalian bones and teeth and Stone Age implements occur in the beds of sand formed by the spring waters during Pleistocene times. Owing to the occasionally disruptive action of the springs, when old "eyes" are reopened, it is not always possible to be sure of the original stratigraphical position of specimens found in these deposits. The most reliable finds are those from below uninterrupted seams of peat.'

Despite deficient data (Dreyer and Lyle, 1931, p. 5, and the Nasionale Museum Register), Oakley (1954a) seems to have obtained information somewhere that *a* tooth of the extinct Sivatherine (*Orangiatherium*) was found between Peat II and Peat III.

3. A horn-core fragment, the type specimen of *Orangiatherium vanrhyni* v. Hoepen, was merely mentioned by van Hoepen (1932). He also mentioned 'a terminal fragment of a large antler and a series of large teeth, which were probably associated'. These specimens, presently housed in the Nasionale Museum and registered under the numbers C 431A, C 431B, and C 426 respectively, are derived from the farm Tierfontein, on the Vet River, 9 miles from Port Allan (personal communication from the Director of the Museum, Dr. A. C. Hoffman) (fig. 18).

4. Specimen F 39 (Archaeological Survey of the Union of South Africa, Johannesburg) is stated by Cooke (1949) to be derived from 'an unknown locality in the Vaal River basin'. This is the type specimen of *Griguatherium haughtoni* Cooke.

5. Two Sivatherine upper milk molars were identified in the collection of specimens from Cornelia, in the Nasionale Museum, Bloemfontein, by one of us (R.S.): these specimens are not registered and are allocated B^1 and B^2 by the authors.

The Cornelia site consists of a large erosional area adjacent to a small branch of the Vaal River. Specimens are found on the floors and on the sides of 'dongas' (eroded clefts) which are washed by seasonal rains and partly covered by flooding of the nearby river, and consequently there are numerous redepositions. The surface consists of hardened calcited sand which rests on varying projections of Karoo formations. A typical view of the site is shown in plate 5 of Oakley's above-mentioned paper (1954a).

B. List of Material and Description

MMK	3685	:	Isolated left M^3—Vaal River (? Waldeck's Plant).
C	1492	:	Cast of occlusal portion of left M_2—Florisbad.
C	426	:	4 isolated upper molars (right M^2 and M^3, left M_1 and M^2)—Tierfontein.
C	431	:	Left posterior horn-core and a right (?) anterior horn-core (ibid.).
F	39	:	Stated to be an isolated anterior pillar of a lower left M_2 or M_3—Vaal River (unknown locality).
B^1 and B^2		:	Isolated right DM^3 and DM^4—Cornelia.

I. HORN-CORES

C 431

There are two specimens marked C 431 from *Tierfontein*. The one is an almost complete posterior horn-core with the tip missing, and this is here designated C 431 A. The other, C 431 B, is a fragment of an anterior horn, and not a part of A.

C 431 A (plate 29(*c*), (*d*))

This is a left posterior horn-core (*vide infra*, 'Discussion'), the base of which is pear-shaped, the narrower portion being anterior. The apex of the hollowed-out portion of the base, formed by sinuses, is 27 cm. distant from the broken edge of the base. From the base, the anterior border runs outwards in a gentle arc towards the first knob, then upwards and slightly medially and then laterally, giving the broad surface of the horn a double twist.

The horn is flattened from side to side opposite the first and second knobs, but above these it tends to bulge where the anterior border becomes rounder.

Grooves on antero-medial surface (cf. Old. 3.53)

From the base there are three fairly deep and broad grooves starting near the front at almost a single point and running obliquely up and back at an angle of about 45°. The most medial groove ends in a trifurcation at the posterior border opposite the first knob. Along the antero-lateral border, at the base of the broken-off flange, three deep grooves pass vertically up parallel to the border. Just below the first knob they tend to deviate from each other, the anterior one running along the anterior border and, passing behind (lateral to) the second knob, it divides into a number of smaller grooves running up almost parallel to each other towards the tip.

Between the levels of the first and second knobs there are four other deep main grooves on the convex surface which run up this surface fairly parallel to each other. The posterior one divides into three just below the level of the second knob, and these then pass towards the posterior border and run laterally.

The anterior border in the region of the flange has two irregular rough tuberosities with numerous vascular foramina. There are, in all, three knobs, very crinkly in appearance and fairly evenly spaced from each other. Between them are two small raised irregular tuberosities.

Circumference at base	*c*. 360
Circumference between flange and knob 2 ..	*c*. 345
Circumference 100 mm. above knob 2	258
Circumference at knob 3	255
Circumference at tip	—
Total length	570+

	A–P	*Side-to-side*
Base	c. 135	c. 87
Between flange and knob 2	137	79
Above knob 2 (100 mm.)	93	71
At knob 3	97	65
At tip	—	—

TABLE 26. Measurements of C 431 A (mm.).

C 431 B (plate 29(*a*), (*b*))

This is an anterior horn, probably right (if the grooves are taken to be on the medial side). The base is flat from side to side and rather triangular with the broad end posterior. Hollowing-out the base are three cranial sinuses.

The medial surface is extremely irregular with numerous ridges formed by deep grooves. The grooves are deeper anteriorly and commence at the base of the anterior border and pass in an inverted triangular fashion, the anterior grooves being vertical and the posterior oblique. The anterior groove branches about half-way up. The posterior part of the medial surface is roughened by small, shallow grooves. The anterior border has a knob just above the base—it has a cauliflower appearance and is distorted by (? vascular) grooves. The top of the anterior border has another similar knob. The superior surface is very irregular and grooved, the central portion being smooth. The posterior border is concave, the upper end passing backwards and there is one small protuberance at the base and one at the upper end. The outer surface is rather smooth with a single deep groove near and parallel to the anterior border.

Circumference at base		280
Circumference at tip		320
Total length: Anterior		c. 220
Posterior		c. 170
	A–P	*Side-to-side*
Base	c. 111	c. 70
Middle (opposite knob)	113	55
Tip	123	61·5

TABLE 27. Measurements of C 431 B (mm.).

2. TEETH

MMK 3685 (plate 25)

An isolated upper molar in a medium stage of wear, with the roots broken off near the base. This is the type specimen of *Griquatherium cingulatum* Haughton. Although it was originally described as a second molar (Haughton, 1922), and stated by Cooke (1949) to be either a M^2 or a M^3, it is here considered to be unquestionably a third molar because of the relative decrease of the lingualward projection of the posterior lingual pillar compared to the anterior one (*vide infra*).

Buccal surface. Each pillar has a marked cingulum, that of the anterior pillar leading to the broad base of the rounded marked parastyle. The central median costa of the paracone is fairly distinct, the bulge commencing about half-way to the occlusal surface.

The mesostyle is distinctly prominent, projecting out markedly in an anterior direction from the surface of the pillar and having a broad base continuous with the cingulum of the posterior pillar on the one side and with the cingulum of the anterior pillar on the other side, though in the latter there is a slight vertical groove partly separating them. The vertical median costa of the metacone is narrow and hardly prominent, commencing near the base just above the rolled edge of the cingulum. Posteriorly, the cingulum of the posterior pillar is continuous with the bulging base of the short metastyle.

Lingual surface. The enamel is rather rugose. On the anterior pillar there is a marked rounded cingulum, the lower border (the one towards the occlusal surface) of which increases in thickness on the anterior surface producing an unusually long, rolled and ridged protostyle. The cingulum of the posterior pillar is relatively small and almost absent in the region of the entostyle. On the posterior surface of the posterior pillar the actual cingulum remains small and ridged but a distinct elongated crest forms an unusual hypostyle. The lingual surface slopes towards the occlusal surface at an acute angle from the cingulum, but near the occlusal surface the angulation changes and the lingual surface tends to become slightly more vertical. The slope of the buccal surface on the other hand is almost vertical.

Occlusal surface. The central pits have widely separated enamel surfaces, the pit of the anterior pillar being acutely V-shaped and closed anteriorly by the anterior limb of the protocone. The central pit of the posterior pillar has a more obtuse V-shape, being closed posteriorly in the region of the metastyle, but open anteriorly and continuous with the space between the enamel surface of the contiguous side of the protocone and the hypocone. The occlusal surface of the posterior pillar is abnormally longer than that of the anterior, the ratio being 114.4 (table 28).

Measurements (mm.) and indices	*Sivatheriinae* M^2 (*Mean*)	M^3 (*Mean*)	*MMK 3685*
$\frac{\text{Occlusal length posterior pillar}}{\text{Occlusal length anterior pillar}} \times 100$ ..	100·2	83·9	114·4
$\frac{\text{Maximum breadth posterior pillar}}{\text{Maximum breadth anterior pillar}} \times 100$ ..	99·1	91·1	91·1
Maximum tooth length	47·6	51·5	53·8
Maximum tooth breadth	49·7	48·7	54·6

Table 28

From the table, the ratio of the breadth of the posterior pillar relative to that of the anterior pillar corresponds closer to that of four other Sivatherine M^3 than to that of two Sivatherine M^2. From observations on the extant material this ratio in M^3 is a very constant one, and consequently, despite the fact that the ratio for the relative occlusal length appear nearer to that of M^2, the authors consider that MMK 3685 is a M^3. The length and the breadth of the tooth are at the outer limits of the range of Sivatherines (tables 28, 40).

C 1492 (*Cast*)

This is a plaster reproduction of the occlusal portion of the crown of a left M_2. Observations on the cingulum are impossible and what can be made out from the enamel of the cast, it appears to be fairly rugose. The tooth does not appear to be in an advanced stage of wear.

Lingual surface. There is a prominent metastylid and the buccal enamel of the metaconid is continuous with the lingual enamel of the entoconid. The parastylid is slightly prominent. The central costa of the metaconid appears rather flattened.

Occlusal surface. The anterior pillar is more rounded than the posterior pillar on the buccal aspect; the central pit of the anterior pillar is ill-defined, but that of the posterior pillar shows a fairly wide central portion, narrow anteriorly and broad posteriorly.

C 426

This number is given to four upper molars. The authors have subdivided them into A, B, C and D which will be entered in the register of the Nasionale Museum, Bloemfontein. A and B belong to the same individual because of the obvious contact surfaces.

C 426 A (plates 26(*a*); 27(*a*); 28(*a*))

This is a right M^3 in an extreme degree of wear. Part of the paracone is missing.

Buccal surface. A cingulum can be seen, especially in the region of the base of the metastyle where it is considerably heaped up. There is no cingulum in the region of the base of the mesostyle and the surface between meso- and metastyle has been hollowed out, in the same 'W' formation as other teeth described previously: there is a slight bulge in the region which leads up to the apex of the metacone. The paracone is almost completely absent.

Lingual surface. Finely rugose. On the hypocone the rugosity is extremely fine with additional transverse striations. On the anterior aspect of the protocone the enamel is raised slightly at one spot, but the rest of this surface is extremely smooth due to contact pressure, and this wear has even extended on to the base of the root in this region. On the hypocone there is a very slight cingulum. On the protocone, the cingulum is slightly more marked, but still negligible. On the protocone too, the lingual surface bulges slightly above the crown-root junction, and it can be seen to slope towards the apex in a buccal direction. The posterior surface of the hypocone is worn right down to the crown-root junction, only a small piece of enamel being visible here. Here also, the wear has extended on to the root.

Occlusal surface. Despite the marked wear, the central pits are obvious, the enamel edges of each pit of the anterior and posterior pillars being separated to a fair degree. In the anterior pillar, the pit has an L-shape, the upright of the 'L' extending right up to the parastyle, which is broken off. However a small island of enamel belonging to this pit can be seen extending towards the mesostyle, but it is separated from the L-shaped portion by dentine which is hollowed out by wear. The pit of the posterior pillar is irregular in shape, the lingual aspect having its enamel thrown into two folds which project into the centre of the pit, and the extremities of the pit extend towards metastyle and mesostyle.

The dentine is particularly hollowed out between the enamel of the lingual surface and that of the central pit. On each occlusal surface can be seen striations which in some places are almost distinct scratches indicating a side-to-side chewing movement of the jaws. The shape of the enamel of the lingual surface viewed from the occlusal side is arc-shaped for both cones, the arc of the hypocone being more flattened than that of the protocone.

Roots. Despite the marked fragmentation, it is possible to identify three roots. The lingual root being composed of two massive pillars joined by a plate, and the anterior pillar being the larger. The posterior buccal root is triangular in shape, while the anterior is broken off at its base and fragmented so that its shape cannot be identified.

C 426 B (plates 26(*b*); 27(*b*); 28(*b*))

This is a right M^2 which is very fragmented, so that only a portion of the enamel of the hypocone on the lingual surface is present, while that of the protocone is absent. Both the metacone and the paracone are missing.

Lingual surface. Rugosity is fairly marked in parts, and there is a small cingulum which tends to have a rounded bulge below it. The anterior surface of the protocone shows some ridging of the enamel just below the small cingulum (protostyle) while the rest of this surface, which is only represented by a small fragment, is very smooth due to contact wear. A small piece of the central pit of the anterior pillar is present, the enamel of the two sides of the pit being separated to a fair degree. The *roots* are represented only by a portion of the lingual root.

C 426 C (plates 26(*d*); 28(*c*))

A left M^2 which is a badly fragmented tooth with only protocone and hypocone and a portion of the lingual root present.

Lingual surface. Rather rugose, with a poorly defined cingulum on the hypocone and a well-defined cingulum on the protocone. On the lingual surface of the protocone, near the occlusal surface, is a ridge of enamel parallel to the cingulum. There is no bulge above either cingulum. The lingual surface of the protocone slopes only slightly towards the apex, while that of the hypocone seems to have a slightly more marked slope. The shape of the lingual enamel of the occlusal surface is arc-shaped for both cones. On the anterior surface of the protocone the enamel shows a slight horizontal ridge (protostyle) but most of the surface is smooth by contact wear. The enamel of the hypocone ends abruptly at the posterior surface and this surface is hollowed out and appears to be worn smooth by contact with the adjacent tooth. This appearance is not uncommon in giraffids.

Occlusal surface. The hollowed-out pits are irregular in shape, the enamel of the lingual and buccal lips of the pit being fairly separated. Because of the absence of parastyle, mesostyle and metastyle, it cannot be determined whether there are any separate islands of enamel in those regions which may have been linked to the central pit at an earlier stage of wear.

Roots. Most of the lingual root is present and it has a similar appearance to that previously described for 426 A and B.

C 426 D (plates 26(*c*); 28(*d*))

A left M^1 which is very incomplete, only a portion of the protocone remaining below a very fragmented lingual root. There is a small cingulum and a very slight thickening of the enamel just below the region of the cingulum where the tooth tends to bulge. The general shape and appearance of the protocone is identical to that of C 426 C.

F 39 (plate 27(*c*), (*d*), (*e*))

This is the type specimen of *Griquatherium haughtoni* Cooke 1949. It has been described as an isolated anterior pillar of a lower left molar, either M_2 or M_3 (*vide infra*). It is in an early stage of wear. Although the evidence for the viewpoint that this is half a lower molar is reasonable, peculiarly enough the specimen also presents a number of features which raise considerable doubt of the accuracy of this diagnosis and which could support the proposition that this specimen is an upper premolar. For this purpose it is necessary to compare it directly with Hopefield 4025 and Olduvai F 2989 (plates 45, 15–17). This matter is discussed in detail below, but the authors consider the evidence to be in favour of a left upper premolar and will describe the specimen on that basis as follows.

Buccal surface. The tooth is broken probably just below the crown-root junction, and a portion of the posterior aspect is broken away. The rugosity is fairly coarse. There is a marked rounded parastyle which is separated from the prominent median costa by a broad groove, and the costa in turn is separated from the prominent metastyle by a narrower groove. Near the occlusal surface, the metastyle swings posteriorly in an arc.

Lingual surface. It is coarsely rugose. The tooth is fractured at the crown-root junction and a small rolled cingulum can be seen at the base of the posterior lingual aspect. This appears to be sufficiently localized to warrant being called an entostyle. From the anterior aspect, it is obvious that the enamel of this surface presents a marked 'apron' effect. The lingual surface slopes markedly downwards in a buccal direction to a point approximately at the junction between middle and lower $\frac{1}{3}$ of the tooth. Then the surface tends to slope more vertically to the occlusal surface, so that the general effect is that the upper $\frac{2}{3}$ of the tooth has a marked lingual bulge. This lingual bulge is the most prominent observed in the whole series of African Sivatheriinae. This matter will be more fully dealt with in the discussion, but it is here noted that an X-ray of the tooth (plate 27(*c*)) indicates internal vertical fracture lines, which may have been caused by intrusive compressing breccia. This may be an explanation for some of the excessive bulging observed.

Occlusal surface. The central pit is fairly wide and open posteriorly, while anteriorly the two enamel surfaces are in continuity with each other.

Posterior surface. A large piece of the enamel near the buccal aspect is broken away, especially from the upper $\frac{2}{3}$ of the tooth. But sufficient of the enamel is present near the occlusal surface to 'close' the lingual and buccal enamel crescents of the protocone. There is also sufficient enamel on the lingual surface to indicate that it is extending without interruption well towards the buccal aspect: this is further back than would be expected if the enamel were to be continued on to the contiguous surface of another pillar (on the alternative supposition that this may have been a lower molar). The enamel is heaped up slightly in the region of the protostyle.

Morphologically it may however be compared favourably with the anterior pillar of M_2 and M_3 of Olduvai 92 (BK II, 1952). On the other hand, if the probability of the dimensions of F 39 is calculated by the *t* test in respect of its being a M_2 or M_3, the following is obtained:

On the basis of	*Value of P* F 39 = ? M_2	F 39 = ? M_3
Occlusal length of anterior pillar ..	·05	·1
Maximum breadth of anterior pillar	·4	·3
Occlusal breadth of anterior pillar..	·8	·6
Buccal height of anterior pillar ..	·01	·01

Because of the large dimensions of this 'pillar' (on the alternative supposition that it is a lower molar), the available measurements have been utilized to reconstruct the whole tooth by a comparison with M_2 or M_3 of other known Sivatheriinae. Calculated on this basis, the Tr./A–P index of F 39 would be:

	M_2	M_3
F 39	64·1	46·1
Mean of Sivatheriinae ..	70·0	49·7

and the ratio $\frac{\textit{Occlusal length of anterior pillar}}{\textit{Maximum breadth of tooth}} \times 100$:

F 39	81·2
Mean of 12 Sivatheriinae M_2 ..	74·5
Mean of 10 Sivatheriinae M_3 ..	75·2

Consequently, it is reasonable to state that one cannot assign F 39 as a definite M_2 or M_3: it is furthermore clear that from the point of view of the length and breadth of the tooth (table 29), it is unlikely to be an anterior pillar of a lower molar. Its height is greater than that of any tooth in the available series (see also 'Discussion').

Sivatheriinae		*Anterior pillar: occlusal length* mm.	*Maximum tooth length* mm.	*Anterior pillar: maximum breadth* mm.	*Maximum tooth breadth* mm.
M_2 (mean of 12 specimens)	..	26·0	51·2	34·9	35·7
M_3 (mean of 10 specimens)	..	25·0	68·6	33·3	33·6
F 39 Actual measurements	..	32·5		*c.* 40	
Inferred measurements:					
If M_2 ..	..		64·0		41·0
If M_3 ..	..		87·5		40·3

TABLE 29

B¹ and B²

These two teeth are both from one site, probably Cornelia, but there are no records available concerning their discovery. The one tooth B¹ has three distinct roots, one lingual and two buccal, and is therefore an upper molar. In B² the roots are broken away and the tooth is only just commencing wear on proto- and paracone. It is also obvious that both teeth belong to the same jaw and the same side because of the exact fit of their contiguous surfaces. Because of, first, the small size of the root in B¹, secondly, of the hollowness of the root and the tooth, thirdly, of the thinness of the cement and enamel, and fourthly, of the general appearance of B¹ and B², it is considered that these teeth are deciduous. Consequently, B¹ is diagnosed a right DM^3 and B² is a right DM^4.

B¹ (plate 30(*a*), (*c*), (*e*))

Right DM^3. It is in early wear

Buccal surface. Small cingulum present. Rugosity very fine. Metastyle, mesostyle and parastyle have a very obvious rib-like effect, the parastyle being the largest of the three styles and being decisively rounded and separated from the lingual surface of the paracone by a distinct cleft. The ridge leading up to the apex of the paracone is more obvious than that leading up to the apex of the metacone, which is almost absent. The appearance is typical of the Family, the surface having an undulating effect, especially when seen from the lingual or the buccal aspect, the crests being formed by the apices of the paracone and protocone, and of the hypocone and the metacone, while the depressions are opposite parastyle, mesostyle and metastyle.

Lingual surface. The protocone has an obvious cingulum, while that of the hypocone is less obvious. On the antero-lingual aspect the enamel is heaped up and forms a ridge (protostyle). Similarly on the postero-lingual aspect of the hypocone, there is another ridge of enamel (hypostyle), but this is very small and less extensive than the protostyle. The surface is finely rugose. Just below each cingulum, there is a bulge which is less marked on the hypocone than on the protocone, and from this bulge the lingual surface slopes fairly acutely towards the apex. From the anterior and posterior aspects, the crown-root junction has an irregular line which is 'apron-like', as in the Hopefield upper teeth.

Occlusal surface. The protocone is quite separate from the hypocone but the central pits of the two pillars are continuous opposite the mesostyle, and it can be seen that the separation of the pits would have been caused at a later stage of wear by the hypocone going to meet the paracone to form the metaconule. The lingual and buccal lips of the pits are widely separated, maximally at the centre of each pillar. The meeting of the protocone and the paracone takes place at the parastyle where their dentine and enamel surfaces are continuous. But the meeting of the hypocone and metacone is only by contact of their enamel surfaces.

Roots. The lingual root is rather small and oval-shaped, the separation into the two thickened portions of the root being hardly noticeable. The cement is very thin, the root and the tooth being completely hollow. The two buccal roots are thin and hollowed although the cement is thicker than in the lingual root; the posterior one is triangular and the anterior one is oval in shape.

B^2 (plate 30(*b*), (*d*), (*f*))

Right DM^4.

Buccal surface. There is a slight cingulum present on the hypocone and it leads up to a very marked mesostyle and a slightly less marked metastyle. The parastyle is prominent and rounded, and it has a small nodular excrescence on its buccal aspect. The mesostyle is somewhat split by a vertical furrow. The buccal aspect of the paracone is much more marked than that of the metacone The buccal surface of the metacone is distinctly spatulate-shaped as is commonly found in milk dentitions.

Lingual surface. Finely rugose. The hypocone has a slight bulging cingulum from which the lingual surface slopes rather sharply to the apex. Although the protocone is rather fragmented at its base, there seems to have been no cingulum, and the lingual surface also slopes rather sharply towards the apex. On the anterior surface, the enamel is thrown into a small ridge (protostyle) just above the crown-root junction.

Occlusal surface. The hypocone and metacone are just beginning to wear, whereas the protocone and paracone are worn to a more marked degree. All four cones are separated, their fusion only occurring between the hypocone and metacone near the metastyle, and between the protocone and paracone near the parastyle, while paracone and metacone are almost completely fused on the buccal surface medial to the mesostyle. Consequently, the central pits are 'wide open' although the two cones of each pillar have fused at the base of each pit at the base of the tooth.

Roots. No roots present. They have been broken off. The tooth is hollowed out.

Shape. The protocone is V-shaped and the hypocone is slightly more arched and broader. The paracone is almost a straight line while the metacone is spatulate-shaped.

CHAPTER 3

MAKAPANSGAT (NORTHERN TRANSVAAL, UNION OF SOUTH AFRICA)

The various discoveries in and the geology of the Limeworks Cave in the Makapan Valley have been fully described by Dart (1954), Oakley (1954b), Brain, van Riet Lowe and Dart (1955), Howell (1955), Brain (1957, 1958), and Wells and Cooke (1957) in whose publications further references may be obtained.

All the material described here is on loan from the Bernard Price Institute for Palaeontological Research (Johannesburg), and is derived from the Limeworks dumps wherein out of 1,862 skull remains already recovered some 30 belong to Giraffids (Dart, 1957). However one specimen, M 553 B^1, is from an unknown locality in the Makapan Valley, 'and probably from one of the limeworks' (Cooke and Wells, 1947). Some of the material is still heavily filled with calcified grey cave breccia.

The material received for study may be divided into two major groups: the first group consists of giraffid teeth referable to *Giraffa*, the determination of the species of which will be mentioned later. The second group is composed of fragments of the dentition and of the jaws of Sivatheriinae. Both groups were recovered from the same deposits, and from the nature of the breccia it is probable that they were contemporaneous in so far as the limits of the formation of the breccia are widely separated by a large period of time.

List of Material

A. GIRAFFA

(1) *Upper dentition*

(*a*) Milk	M 646	right DM^2
	M 944	left DM^2
	M 536	left DM^3
	M 263	fragment of right maxilla with DM^3—M^1
	M 533	right DM^4
	M 535	left DM^4
	M 1115	left DM^4
(*b*) Adult	M 532	left P^2
	M 531	left P^3
	M 264	right P^3
	M 1114	right P^3
	M 552	right M^1
	M 551	left M^1
	M 550	fragment of maxilla with left M^2
	M 528	fragment of maxilla with left M^2—M^3

(2) *Lower dentition*

(*a*) Milk	M 939	fragment of left mandible, with DM_2 and DM_3
	M 540	fragment of right mandible, with DM_2—DM_4
(*b*) Adult	M 936	right M_2
	M 942 and M 1113	joined fragments of right M_2
	M 938	fragment of right mandible with M_3

B. SIVATHERIINAE

(1) *Upper dentition*

	Milk	M 937	isolated left DM^3 or DM^4
		M 524	right, probably DM^3
		M 941	right, DM^3 or DM^4

(2) *Lower dentition*

(*a*)	Milk	M 525	left DM_3
		M 539 B	fragment of right mandible with DM_4
(*b*)	Adult	M 527	incisor
		M 1116	incisor
		M 553 A	fragment of left mandible with P_2
		M 553 B	fragment of right mandible with $P_2—P_3$
		M 553 B[1]	fragment of left mandible with $M_1—M_2$
		M 943	isolated pillar of right M_2
		(See also Appendix.)	

Description

A. Giraffa

The general appearance of these teeth is the same as that of the extant *Giraffa camelopardalis* and nothing can be gained by describing each specimen in detail. The only variations that may be noted are minor individual ones, namely, those of irregularity of enamel ridges present in some and not in others, the presence of entostyle and parastyle, of ectostylid and parastylid and other variations which are also found in the non-fossilized extant material.

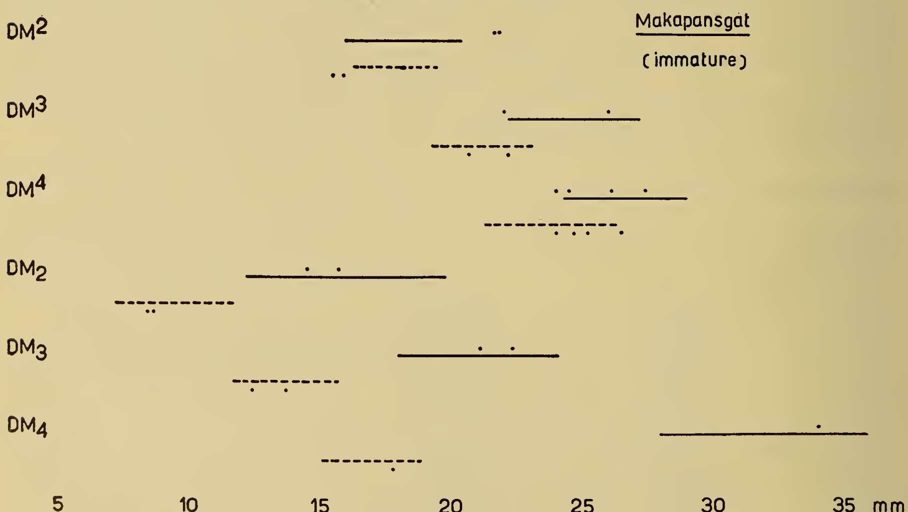

Fig. 19. Dimensions of deciduous teeth of Makapansgat *Giraffa* plotted against ranges of variation in modern *Giraffa camelopardalis*.
—— = A–P length. ------ = Transverse (breadth). . = Makapansgat specimens.

(1) UPPER DENTITION

(*a*) *Milk teeth*

M 646 *and* **M 944** (plate 31(*a*), (*i*), (*q*); 31 (*b*), (*j*), (*r*))

These are deciduous upper second molars, 944 being left and 646 being right. They are in the same stage of early wear and are identical to each other. It is considered that they probably belong to the jaw of the same individual.

M 536 (plate 31(*c*), (*k*), (*s*))

An isolated left upper deciduous third molar, the posterior buccal root of which is broken off at the base, while the other roots are broken about half-way down. The tooth is in fairly advanced wear.

M 263 (plates 32(*g*); 33(*d*); 34(*d*))

This is a fragment of the right upper jaw containing DM^3, DM^4 and M^1. The teeth are in early stage of wear, DM^3 being in a more advanced stage than M^1 whose posterior part of the posterior pillar is just commencing wear.

In spite of their similar appearance and their similar degree of wear, it is unlikely that 944 and 536 (left DM^2 and DM^3 respectively) on the one hand, and 646 and 263 (right DM^2 and DM^3 respectively) on the other hand belong to a single individual. The Dental Index has been calculated (see Section I, chapter 5) for both pairs of teeth, and compared with the corresponding range of variation for the extant *G. camelopardalis*. As seen in the following table, all three ratios (length, breadth and Tr./A–P index ratio) fall outside the respective ranges for the extant material:

	Dental index		*Tr./A–P*
	Length index	*Breadth index*	*index*
944/536	83·3	71·7	85·7
646/263	99·0	74·8	75·7
Range of DM^2/DM^3 in *G. camelopardalis*	62·7–81·9	75·5–92·3	94·0–127·4

TABLE 30

M 533 (plate 31(*d*), (*l*), (*t*))

It is an isolated right upper deciduous fourth molar, with the roots broken off at the base. The anterior pillar has just commenced wear.

M 535 (plate 31(*e*), (*m*), (*u*))

It is an isolated left upper deciduous fourth molar, with the anterior buccal root broken off at the base, while the two other roots are broken about half-way down.

M 1115 (plate 31(*f*), (*n*), (*v*)

It is an isolated left upper deciduous fourth molar, whose roots are broken off near the base. It is in an early stage of wear.

(*b*) *Adult teeth*

M 532 (plates 33(*f*); 35(*a*), (*e*))

This is a left upper premolar, P^2, in early wear.

Buccal surface. It has the typical appearance of a paracone of an upper premolar. Although there is a vertical furrow on the buccal surface between paracone and metacone, there is no separation on their lingual surface. Between the apex of the paracone and the parastyle, there is a small enamel tubercle. The central pit is irregularly V-shaped being open anteriorly, but closed by a ridge of enamel posteriorly between the protocone and the metacone, while the enamel in the region of the protocone invaginates into the central pit as a double fold.

Lingual surface. The surface is fairly rugose. There is a ridge of enamel opposite the centre of the protocone, while this ridge increases posteriorly to form a broad entostyle.

M 531 (plates 33(*h*); 35(*d*), (*h*))

A left P^3. This is a very worn tooth.

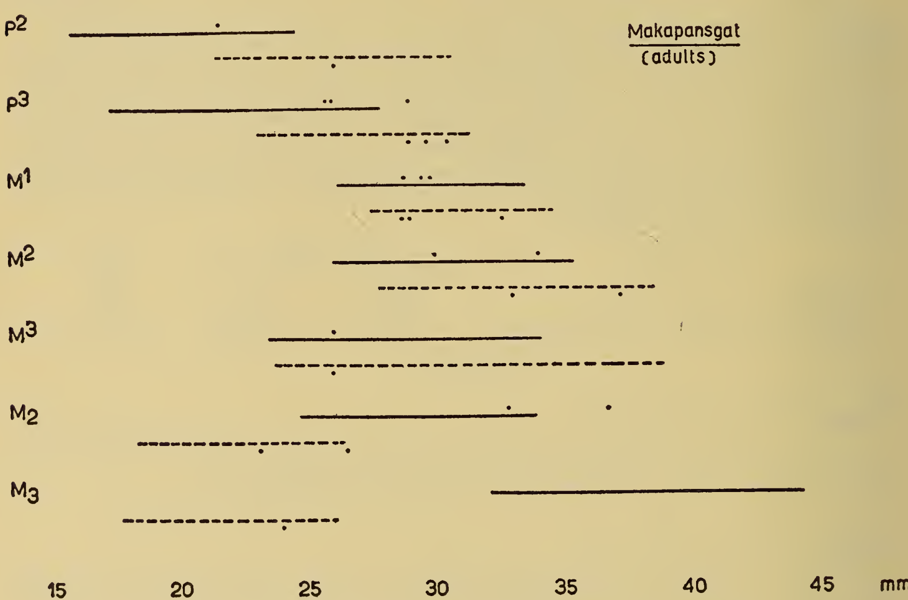

FIG. 20. Dimensions of adult teeth of Makapansgat *Giraffa* plotted against ranges of variation in modern *Giraffa camelopardalis*.
—— = A–P length. ------ = Transverse (breadth). . = Makapansgat specimens.

Lingual surface. A cingulum is present; rugose lines may be seen scattered all over the enamel, but the surface has been smoothed. The enamel bulges just below the cingulum and there are marked bulges at the bases of the parastyle and the metastyle.

Occlusal surface. The central pit is almost obliterated, the enamel of the two sides being in close contact or even fused, and there is a small island of enamel cut off from the central pit in the direction of the metastyle.

The *roots* are very similar in shape to M 1114 (*vide infra*), but they are ever shorter, their tips tapering to a sharp point very rapidly.

M 264 (plates 33(*i*); 35(*b*), (*f*))

A right P^3, which is in very advanced wear. The general appearance is that of M 531, except that the rugosity is more widespread and that the small island of enamel on the occlusal surface which leads up to the metastyle is in contact with the enamel of the rest of the central pit. The parastyle is markedly curved and twisted posteriorly on its own axis, as in M 531 and M 1114. As in M 531 too, the entostyle is not present because the tooth is worn above the level at which it projects in M 1114 (*vide infra*).

Roots. They are rather smaller than in other teeth and there appears to be a constriction at the base of the posterior buccal root.

M 1114 (plates 33(*g*); 35(*c*), (*g*))

A right upper ? third premolar, fragmented and in advanced wear, with the metacone broken off.

Lingual surface. A cingulum is detectable and there is a rounded bulge below it. There is a minute enamel nodule on the antero-lingual aspect in the region of the protostyle. It is fairly rugose. There is a marked entostyle on the posterior part of the lingual surface. Half the buccal surface is missing. The anterior half resembles the paracone of a premolar in that the enamel ridge passing to the apex is thick, rounded and triangular in shape and the enamel is folded to form a prominent parastyle. The central pit is irregularly V-shaped. It narrows towards the parastyle, but broadens out towards the metastyle where the enamel is partly broken away. As mentioned in M 264, M 531 and M 532, the buccal enamel of the protocone evaginates into the central pit and with wear it isolates (M 531, M 264) an island of enamel of the central pit in the region of the metastyle. This feature is common to the premolars in *Giraffa* and Sivatheriinae.

Roots. There are three roots. The lingual root is very broad at the base, triangular in shape, and the two buccal roots are smaller and separated by a V-shaped interval from each other and from the lingual root. The roots are all short. The two buccal roots are broken off half-way.

M 552 (plate 31(*g*), (*o*), (*w*))

An incomplete, isolated right M^1; the roots are broken off at the base. The tooth is in quite early wear.

M 551 (plate 31(*h*), (*p*), (*x*))

It is an isolated left upper molar, M^1, with the roots broken off at the base. Very slight degree of wear can be observed only on the anterior cones of the anterior pillar.

M 550 (plate 34(*f*))

This is a fragment of a maxilla containing a left M^2, while the sockets of the roots of M^1–P^3 are visible. The tooth is very worn especially on the posterior aspect of the posterior pillar where the enamel has disappeared completely. The dentine on the occlusal surface has been hollowed by an unusual type of wear. The maxilla is rather squashed and the empty root sockets are filled with calcite matrix. On the upper aspect of the specimen a portion of the maxillary sinus has remained.

M 528 plates 32(*h*), 33(*e*), 34(*e*))

This is a fragment of maxilla containing left M^2 and M^3 which are in an advanced stage of wear.

(2) LOWER DENTITION

(*a*) *Milk teeth*

M 939 (plate 37(*a*), (*h*), (*k*))

A fragment of a left mandible containing DM_2 and DM_3, and part of the socket of DM_4 is present.

M 540 (plate 37(*b*), (*g*), (*i*))

A fragment of a right mandible containing DM_2–DM_4.

Measurements of mandible opposite talonid of DM_4 (mm.)

Lingual height	40·2
Buccal height	36·3
Thickness	27·0

(*b*) *Adult teeth*

M 936 (plates 32(*e*); 33(*b*); 34(*c*))

A fragmented lower right molar, probably M_2.

M 942 (plates 32(*f*); 33(*c*); 34(*b*))

It is the posterior pillar of a right lower second molar.

M 1113 (plates 32(*f*); 33(*c*); 34(*b*))

It is the anterior pillar of a right lower second molar. It and M 942 have identical contact surfaces and fit each other, forming a single tooth.

M 938 (plates 32(*d*); 33(*a*); 34(*a*))

It is a fragment of a mandible containing an erupting M_3 and there is also a socket for the posterior buccal side of the root of a M_2: the posterior root of M 942 fits perfectly into this socket, and it is obvious that M 938 and M 942–M 1113 belong to the same individual.

Determination of the Species of the Makapan Giraffa

It has already been stated (see introduction to the description, chapter 3) that morphologically (non-metrically) these fossil specimens are indistinguish-

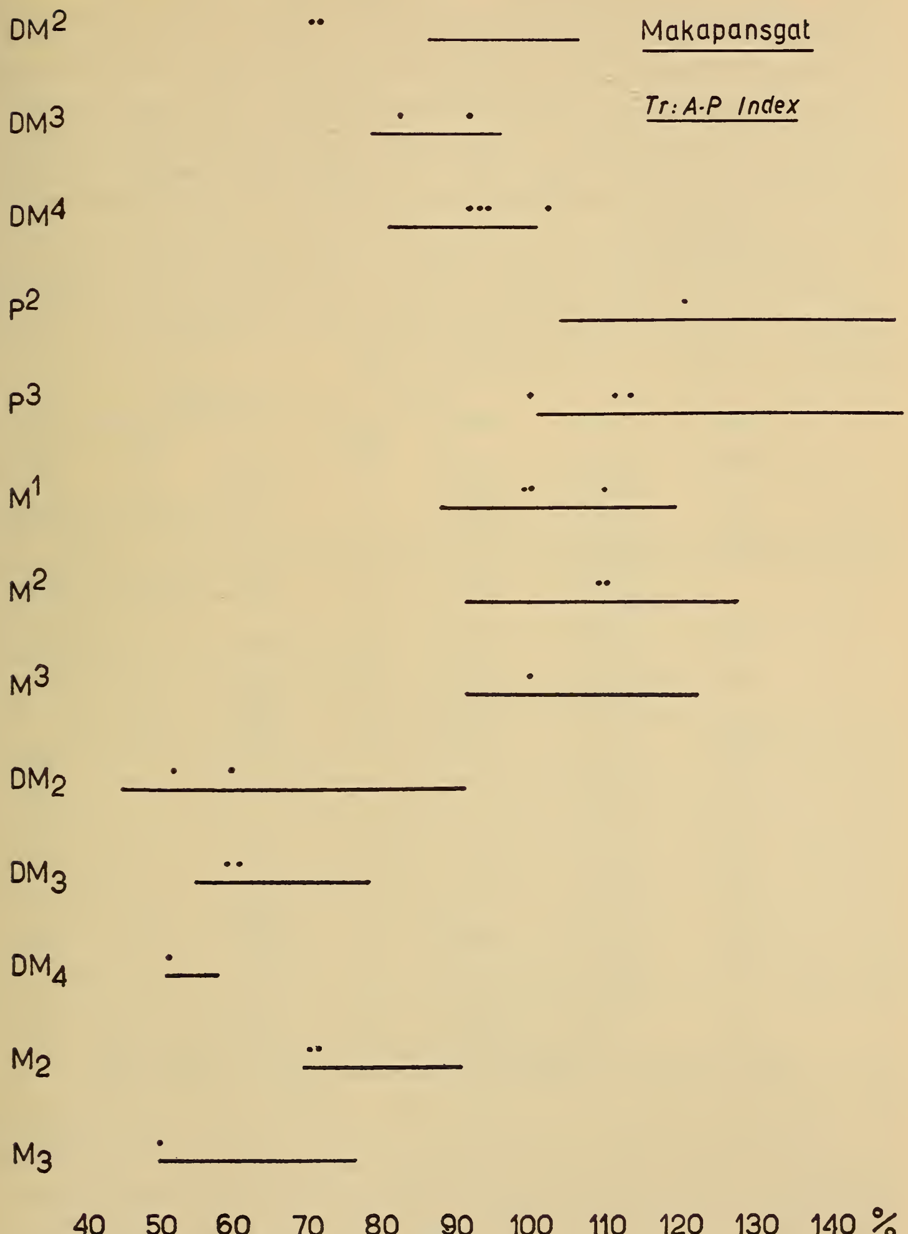

FIG. 21. Transverse/A–P Index of Makapansgat *Giraffa* plotted against ranges of variation in modern *Giraffa camelopardalis*.
● = Makapansgat specimens.

able from the extant *Giraffa camelopardalis*. Statistical analysis of the dimensions of the specimens indicates that in general they fall well within the range of variation of *Giraffa camelopardalis* (figs. 19, 20, 21, table 39). However, it must be pointed out that in quite a number of cases, the dimensions tend to fall towards the lower limit of and even just outside the extant range; while in some cases, they fall beyond the upper end of this range (for instance, length and breadth of M 646, M 944; lengths of M 938, M 942 and M 1113). This distribution raises the possibility that the specimens may belong to another species or subspecies.

Consequently the *t* test was applied to both the A–P and transverse dimensions of each of the specimens. The results of this analysis are given in table 31. It will be seen that the probability (P), i.e. of belonging to *G. camelopardalis*, is less than ·01 (1 %) in only five cases.

		A–P		*Transverse*	
Tooth	*Specimen*	*t-value*	*P smaller than*	*t-value*	*P smaller than*
DM^2	M 646, M 994	3·2156	·01	2·1258	·05
DM^3	M 263, M 536	·5027	·7	·2974	·8
DM^4	M 533, M 263, M 1115, M 535	1·358	·2	1·354	·2
DM_2	M 939, M 540	·2663	·8	1·464	·2
DM_3	M 939, M 540	·9029	·4	·9443	·4
DM_4	M 540	·6874	·5	·6801	·5
P^2	M 532	·3984	·7	·2550	·8
P^3	M 1114, M 264, M 531	4·5118	·01	1·5456	·2
M^1	M 263, M 552, M 551	·58	·6	·791	·5
M^2	M 550, M 528	·1772	·9	2·3455	·02
M^3	M 528	1·9095	·1	2·846	·01
M_2	M 936, M 942, M 1113	3·069	·01	1·074	·3
M_3	M 938	1·6454	·01	·3409	·8

TABLE 31. Results of application of the *t* test to the length and breadth measurements of the teeth of *Giraffa* from Makapansgat. (P = probability)

A further step was to estimate the extent to which these 'abnormal' dimensions occur together in a single population. Because of a probable correlation between transverse and A–P measurements in individual teeth, the probability should only be considered for one or the other measurement, and consequently it has been estimated separately for each dimension. In respect of the A–P dimension, applying the binomial distribution, the probability that in 13 cases, 4 measurements occur on a less than ·01 chance is ·09, which is not highly significant. It is obvious that P, estimated on the basis of the transverse dimension, is still less significant. Therefore there is no basis for placing these specimens in a different species from *G. camelopardalis*.

Furthermore, because the Makapansgat teeth are mainly isolated specimens and the measurements of the majority of the modern specimens were taken on intact jaws, slight differences in the actual measurements probably resulted. This would sufficiently account for the few isolated exceptional results. However it has also been established in other groups of the Hopefield fauna that the Pleistocene fossil representatives of modern species tend to have dimensions (of teeth and skeletal parts) towards the upper end of or just outside ranges of variation of the modern species (Ewer and Singer, 1956; Hooijer and Singer, 1960).

B. SIVATHERIINAE

UPPER DENTITION

Milk

M 937 *and* **M 524**

For the same reasons as given for Cornelia B^1 and B^2, these two teeth are deciduous molars.

(*a*) **M 937** (plate 37(*c*), (*e*), (*j*))

It is either an upper left DM^3 or DM^4. It is unworn.

Buccal surface. There is a cingulum on each of the cones which have a typical spatulated appearance, the paracone being less curved than the metacone. The general appearance is similar to the buccal surface of B^2 from Cornelia, except that the central ridges leading up to the apex of the paracone and of the metacone are much more prominent. The parastyle is broken off.

Lingual surface. The crown-root junction is fragmented, but a cingulum appears to have been present adjacent to this area, and there is a rounded bulge below the cingulum. The enamel is fairly rugose and is thrown into horizontal ridges on the anterior surface of the anterior cone. The lingual surface of the protocone has a thickened pilastering which leads up to the apex. This effect is slightly less marked on the hypocone.

Occlusal surface. The hypocone has a V-shape, while the paracone tends to be slightly more U-shaped. The central pits are open in the region of the mesostyle.

Roots. The lingual root is broken off at the crown-root junction while the other two roots are embedded in a fragment of the maxilla and matrix.

(*b*) **M 524** (plate 37(*d*), (*f*), (*l*))

A right ? DM^3.

Buccal surface. There is a rounded cingulum. The metacone presents a typical spatulated surface, with the mesostyle curving outwards and forwards.

The paracone has a marked central costa which is very broad at the base and which has two vertical furrows near the apex. The parastyle is prominent with a thick rounded base. There are small nodular excrescences on the parastyle which tends to recurve near the apex to give the cone its spatulated shape.

Lingual surface. It is finely rugose. There is a rounded cingulum which is more marked on the protocone and which has a small denticulated ridge of enamel below it. There is a very marked protostyle on the anterior surface. On the posterior surface of the hypocone, the enamel ridge is much less marked and there is no cingulum on this surface. There is a small linear entostyle present.

Occlusal surface. The central pits are wide and open, except in the region of the parastyle where the anterior part of the protocone fuses with the paracone. The hypocone is V-shaped while the protocone is flattened out.

Degree of wear. The anterior pillar and the anterior part of the posterior pillar are slightly worn while the posterior part of the posterior pillar is just beginning to show signs of wear.

M 941

This is either a right DM^3 or DM^4. The roots are broken away, and on the crown only the hypocone is more or less intact. It is in early wear. This tooth shows similar characteristics to those seen on M 937. The lingual surface slopes at a fairly marked angle towards the apex. The buccal surface also slopes but to a lesser degree.

LOWER DENTITION

(*a*) *Milk teeth*

M 525 (plate 32(*a*), (*b*), (*c*))

This is a deciduous tooth and probably a left DM_3 (see Dental Index of M 525/M 539 B (DM_4), *vide infra*). There is a small rounded cingulum which is particularly prominent on the hypoconid. The surface of the tooth is finely rugose and worn; there is a rather large bulge on the cingulum on the posterior aspect of the hypoconid. There is no cingulum in the region of the entostylid where the hypoconid fuses with the entoconid.

Buccal surface. There is a fine groove between the hypoconid and the protoconid. The protoconid has a distinct bulge. Posteriorly the protoconid is fused with the enamel of the entoconid, and the metaconid juts out on the lingual aspect of this fused ridge. Anteriorly, the protoconid is continuous with the parastylid which also juts out at right angles from the enamel ridge, and this, in turn, fuses the protoconid with the parastylid. Consequently, there is a V-shaped depression between parastylid and paraconid on the lingual aspect of the tooth, although the two are fused on the lingual surface about half-way from the occlusal edge of the tooth. There is also a U-shaped depression on the lingual side of the protoconid between the projections of paraconid and metaconid, which are fused to each other about two-thirds of the way down from the occlusal edge of the tooth, so that there is a V-shaped interval between them on the lingual surface. There is a small depression between metaconid and entoconid near the occlusal edge. A linear central pit stretches between the hypoconid and the enamel ridge, which links entostylid–to–entoconid–to–protoconid.

There is a small cingulum on the *lingual surface*. There are two hollow *roots*, a posterior one below the hypoconid and an anterior root below the protoconid. A distinct similarity is observed between this tooth and P_3 of M 553 B. The only differences in appearance being that the metaconid projects in a more lingual direction in M 525, and that the enamel ridge forming the central pit of the paraconid in M 553 B is circular, while in M 525 it is more V-shaped, and that the occlusal edge of the lingual surface is not as high in M 525.

M 539 B (plate 38)

This is a fragment of a right mandible containing a DM_4 which has just erupted, and the tip of paracone of M_1 is visible because the surrounding alveolus is broken away.

Buccal surface. The enamel of DM_4 is fairly rugose. There appears to have been a cingulum and there is a large hypostylid and a broken-off ectostylid.

Lingual surface. There is a rounded cingulum. Finely rugose. On the paraconid there is a broad, flattened central costa leading up to the apex of the pillar, while the parastylid and mesostylid are less marked; the parastylid curves slightly inwards at its anterior extremity, so that the surface presents a slightly spatulate appearance. The metaconid has a similar appearance, but anteriorly it fuses with the mesostylid of the anterior cone. The lingual surface of the anterior pillar overlaps that of the posterior pillar which in turn overlaps that of the talonid. The talonid has a very marked central costa leading up to its apex from the cingulum. This pillar is particularly broad at its base so that it appears to occupy most of the surface. The anterior portion of the surface curves slightly inwards, and comes to lie against the metastylid of the posterior cone.

Occlusal surface. The A–P axis of the lingual surface of the posterior cone is at a slight angle to that of the talonid; the anterior portion of this cone is angulated at an even greater angle to that of the posterior cone. The central pits are wide and open, and on the buccal surface of the paraconid the enamel is markedly ridged, so that it projects backwards into the central pit. The buccal cones are V-shaped in occlusal view, the central portion of each surface producing a ridged effect which leads up to the apex of each cone.

Roots. Through the broken mandible the top of the short central root is visible. On X-ray (plate 38(*c*)) the outline of the developing tooth bud of P_4 may be seen, as well as the outline of the alveolar 'pocket' containing M_1 which is still embedded in the mandible.

Measurements of mandible (mm.)

Breadth opposite the talonid ..	32·0
Breadth opposite M_1	34·0
Height opposite the talonid ..	*c.* 47

The Dental Index (see Section I, chapter 5) has been calculated between left DM_3 (M 525) and right DM_4 (M 539 B), in order to determine whether they belong to the same jaw. All three ratios fall well within the range of variation of the corresponding index for the corresponding measurements in extant *G. camelopardalis* and are very close to their mean values.

	Length index	*Breadth index*	*Tr./A–P index*
M 525 / M 539 B ..	60·0	75·6	124·0
G. camelopardalis:			
Mean	63·1	79·7	123·5
Range	55·6–72·3	70·2–92·1	98·7–144

Table 32

(*b*) *Adult teeth*

M 1116 *and* **M 527**

These are two incisors in very early wear; M 527 is at a slightly earlier stage than M 1116. Judging by the slope of the anterior edge of the enamel of the teeth, it would appear that M 1116 belongs to the left side and M 527 is right.

M 1116 (plate 36(*d*), (*e*), (*f*))

Buccal surface. The enamel is finely rugose and there is a distinct cingulum which bulges out on the lingual and the buccal aspect. However, the cingulum is absent on the sides of the tooth. In buccal view, the tooth is rather V-shaped, but the apex of the V (i.e. at the crown-root junction) is flattened, while the upper edges of the V are slightly flanged outwards. The outer surface is convex in a mesio-distal plane.

Lingual surface. The anterior edge of the enamel is spade-shaped, while the posterior edge is irregular (‾|_|‾). The dentine is hollowed out, the edges of the dentine sloping towards a deep central portion; it is slightly worn at its anterior end.

Roots. The root is almost complete and rather oval in shape, being slightly flattened anteriorly, resembling very much the root of Hopefield 4026. Viewed from the side, the crown-root junction has an inverted V-shape.

M 527 (plate 36(*a*), (*b*), (*c*))

This appears to be a right incisor, identical in appearance and shape to M 1116, but being a little broader from side to side and in a mesio-lingual plane at the crown-root junction.

Measurements (*mm.*)	*M 1116*	*M 527*
Total height	*c.* 74	—
Crown (buccal) height	37·4	38·4
Length	22·0	22·7
Maximum height (just above the crown-root junction, i.e. at its highest point)	17·6	17·4

TABLE 33

M 553 A (plates 39(*a*), (*b*); 40)

This is a fragment of a left mandible on which the posterior part of the symphysis menti is present. It contains a P_2 about to erupt as well as the tip of the root and I_1 and the breccia-filled sockets for the tips of I_2 and I_3. There is no evidence of the canine. On the outer aspect, near the front of the fragment, a large foramen mentale is present; it is oval in shape, with rounded edges, and leading from it anteriorly there is a deep groove.

The tip of the canine is approximately opposite the mental foramen which in turn is opposite the posterior end of the symphysis.

The superior border of the fragment is very sharp, while the inferior border is rounded. The medial surface is smooth and convex in shape, while on the outer surface, there is a deep horizontal furrow about one-third of the height below the superior border. The symphysial region is markedly irregular and its posterior end is oval in shape and flattened from above downwards.

P_2

Although partially embedded in the mandible, most of the crown is visible for description.

Buccal surface. Fairly rugose. The crown-root junction is not visible and a cingulum formation cannot be commented on. But the hypoconid is rounded and bulging above the crown-root junction, and slopes gradually towards the apex. It is split vertically by a deep groove which extends down half-way from the occlusal surface.

On the *posterior surface* there is a thickened ridge of enamel, at the lingual end of which the medial portion of the entostylid is broken off.

Lingual surface. This is also fairly rugose, and its prominent feature is the metaconid which bulges out on the surface so that there is a hollow between it and the entoconid. But anteriorly there is only a slight depression between the metaconid and the paraconid; the parastylid is not visible.

Occlusal surface of this unworn tooth is irregular in shape, the highest point being the apex of the protoconid which is still fused with that of the metaconid.

The absent canine is broken off near the tip of the root. All that one can see is its circular shape. It almost occupies the whole breadth of the bone in this region; it is 19 mm. in diameter.

Height opposite anterior end of P_2 (buccal side)	67·7
Height opposite mental foramen	67·2
Maximum thickness opposite P_2	26·5
Distance (direct) between anterior edge of alveolus of P_2 and posterior edge of mental foramen	99·0
Distance between anterior edge of alveolus of P_2 and posterior border of symphysis	102·5

TABLE 34. Measurements of mandible (mm.).

M 553 B (plate 39(*c*), (*d*))

This is a fragment of the right half of a mandible containing P_2 and P_3, and showing a part of the alveolar fossa for P_4. Beyond P_2 the sharp anterior border continues for about 7 cm. to the broken end where there is a vertical fracture. On the buccal aspect of the mandible there is a broad and deep groove which almost disappears opposite P_4: here the buccal surface tends to be almost straight in a vertical direction. The lingual surface is convex and the inferior border is rounded, as in M 553 A.

P_2

It is just erupting and partly broken. Part of its alveolar socket is broken away, so that one can ascertain that it is similar in appearance to P_2 of M 553 A.

P_3

It is still embedded in its bony alveolar socket and only its tip is erupting. Most of the lingual surface of the alveolus is broken off, so that a large part of the crown is visible for study. The *buccal surface* is fairly rugose, while the lingual surface is slightly smoother.

The highest point of the tooth is the protoconid which is shaped like an inverted V, and this cone occupies most of the buccal surface of the tooth. The hypoconid is small and in continuity with the protoconid. Half of the lingual surface is occupied by the entoconid and metaconid, the metaconid being almost at a right angle to the lingual aspect of the protoconid and is fused with it just posterior to the protoconid apex: in this way an irregular L-shaped central pit is formed. Between the metaconid and the paraconid there is a wide interval, the two being joined laterally by a part of the lingual aspect of the protoconid. The metaconid meets the paraconid just above the crown-root junction so that, viewed from the lingual aspect, there is a V-shaped interval between them. The paraconid is angulated at right angles to the A–P axis of the body of the protoconid, while the anterior part of the protoconid is also angulated at right angles to the rest (body) of its own axis. Thus an oval-shaped pit is formed between the protoconid and the parastylid. On the lingual surface, the parastylid is seen as a prominent bulge, the apex of which is at the occlusal junction between the recurved paraconid and the protoconid.

Maximum breadth opposite P_3	35·0
Maximum breadth opposite P_2	27·0
Height opposite anterior end P_2 (buccal side) ..	67·3
Height opposite anterior end P_3 (buccal side) ..	77·4

TABLE 35. Measurements of mandible (mm.).

M 553 B[1] (plate 41)

This specimen was described by Cooke and Wells (1947) as *Griquatherium cingulatum* neotype.

It is a fragment of a left mandible containing M_2 and M_1. Posterior to M_2, where M_3 would have been, there is a mass of limestone matrix. Anterior to M_1 the posterior cones of P_4 are just erupting through the alveolar surface, and there is a vertical fracture through the anterior cones, indicating the early stage of eruption of P_4. On X-ray, the socket for the anterior root of M_3 is seen filled with breccia. The roots of the other teeth are very long, penetrating more than two-thirds of the height of the body of the mandible. The crown-root junction is well below the alveolar margin.

M_2

The tooth is in early wear, and hypsodont in appearance. It slopes slightly anteriorly from below upwards. The buccal surface is fairly rugose and there is no cingulum formation visible. The enamel has slight irregularities on it, and there is a small protostylid. Looking at the posterior surface, it can be seen that the buccal surface has quite a marked slope towards the apex, and that, in similar fashion, the lingual surface has an even more marked slope, especially in the region of the entoconid.

Lingual surface. The crown-root junction is not visible, but there appears to be no, or very little, cingulum formation. The surface is fairly rugose. The rugose lines of the enamel tend to radiate upwards from the crown-root junction and forwards and backwards from the central costa in a fan-shaped fashion. The entostylid is broken off, and the anterior portion of the entoconid is in contiguity with the metastylid at the occlusal surface, but the enamel on their lingual surfaces tends to fuse lower down. The metastylid is partly broken off but it is fairly marked, while the parastylid is short and blade-like, and it is sharply angulated anteriorly. The central costa passing from the crown-root junction to the apex of the metaconid is much thicker and more marked than that of the entoconid.

Occlusal surface. The four cones are almost completely separated from each other. The protoconid is contiguous with the paraconid at the apex of the parastylid, while the hypoconid meets the entoconid in the region of the entostylid. But the central pits are not completely closed off where the anterior pair of cones meets the posterior pair of cones, and the medial and lateral lips of the central pits are rather widely separated. At this early stage of wear, the dentine appears as a narrow strip in each cone, and the protoconid and the hypoconid are V-shaped, while the metaconid and the entoconid tend to be more flattened.

M_1

It is in a slightly more advanced stage of wear than M_2, and has the identical appearance of M_2, except that the dentine is thicker in each cone.

Height opposite anterior pillar M_1 (lingual aspect)	..	78·5
Height opposite anterior pillar M_1 (buccal aspect)	..	75·0
Breadth opposite anterior pillar M_1 (maximum) ..	..	49·7
Breadth opposite anterior pillar M_2 (maximum) ..	..	55·5

TABLE 36. Measurements of mandible M 553 B^1 (mm.).

Note.—M 553 A and M 553 B must belong to opposite sides of the same lower jaw, because of:

(1) the proximity of the discovery;
(2) the same dental age, judging by the stage of eruption; and
(3) the similar size and shape of corresponding regions of their fragments and of their teeth (P_2).

That portion of M 553 B which we consider to correspond to the posterior portion of A has been reconstructed (fig. 22). It appears obvious that M 553 A must belong to M 553 B^1; this is in accordance with the degree of eruption of P_4 and the degree of wear of M_1 and M_2 in the latter fragment. Consequently these three fragments must belong to the same individual. (See also 'Appendix'.)

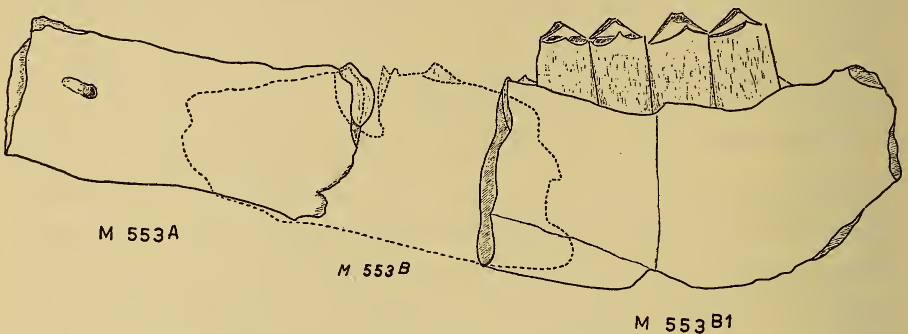

FIG. 22. Reconstructed mandible of the Makapansgat *Sivatherium olduvaiense*.

M 943

This is a fragmented posterior pillar of a right M_2. It has all the features of the corresponding pillar of M_2 of M 553 B^1, but it shows more clearly the groove separating the hypoconid and the entoconid on the posterior surface, just above the point where they fuse. The degree of wear and the general features are so similar to the above corresponding specimen that they could almost be considered to belong to the same jaw.

The lingual surface has a large piece of enamel broken off; the whole of the buccal surface may be measured because the tooth is not embedded in its jaw (table 40).

CHAPTER 4

HOPEFIELD (CAPE PROVINCE, UNION OF SOUTH AFRICA)

The description of the geological features of the fossiliferous site on the farm 'Elandsfontein', near Hopefield, 60 miles north-west of Cape Town (fig. 23) has been recorded previously (Drennan, 1954; Singer, 1954; Mabbutt, 1956). All the material, referred to as 'the Hopefield specimens' have been recovered from the site and are now housed in the S.A. Museum.

No stratification has been found on the site which consists of approximately 2 square miles (5 km.[2]). 'The site lies in the sand veld between the Sout River and the Langebaan-Saldanha Lagoon. This site is 300 feet above sea-level and is divided into wind-scoured kloofs or depressions by sand-dunes which are either drifting or, where covered by vegetation, stationary. Ridges of

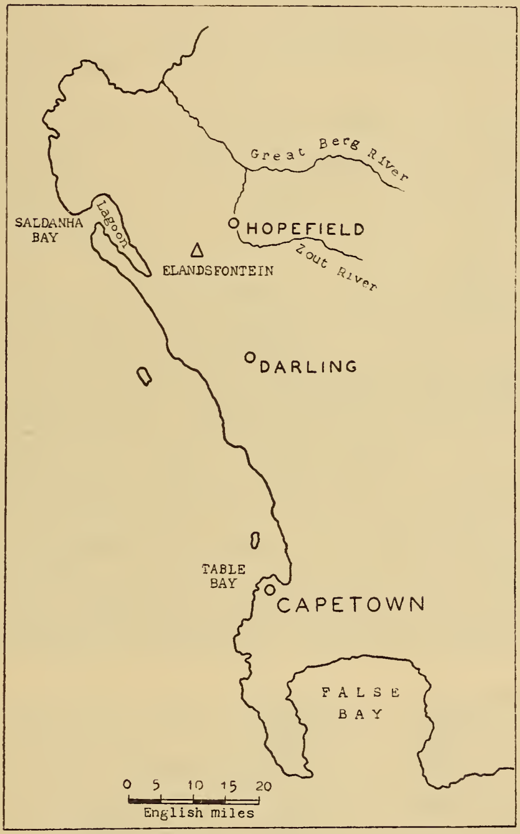

Fig. 23. Map indicating the Elandsfontein fossil site, near Hopefield.

ferricrete cut diagonally across the length of the site, and in places the dunes are capped by massive calcrete mounds or flat boulders of partly silicified surface limestone. Softer, cellular calcretes are found in certain places at the lowest parts of the depressions. The tortuous courses of the ferricrete ridges indicate that they are the indurated lower flanks of old sand-dunes* now

* Recent research by Mr. D. Needham, University of Cape Town, tends to contradict that there were sand-dunes, in the geological sense, originally present. Convincing evidence indicates that the modern 'dunes' are the result of a recent 'heaping-up' of the tertiary marine-deposited sands.

stripped bare of the sand walls. This ferruginization is usually associated with moist ground conditions, a fairly high stable water-table and an abundance of vegetable acids in the soil. It seems that this fossil site was at one time a large vlei or lagoon along the edge of which animals roamed.' (Singer and Keen, 1955).

The movement of the present sand-dunes uncover the calcareous floors from which the fossils and artefacts are recovered.

The majority of the giraffid teeth as well as the cranial fragments have been recovered from different localities on the 'Main site'. However, fragments 4029, 4029 A, 4029 B and 4374 were discovered on a ferricrete deposit in site E–extension (Tex. 1). Further tooth fragments (4030, 4030 A and 4031) were found on and near a ferruginous plateau in 'Buffalo Bay', less than 50 yards from E–extension, but separated from it by a large sand-dune, and it is quite likely that the ferricretes of the two localities are in continuity through the sand-dune.

As a matte of interest, specimens 4029 (heavily encrusted with ferricrete) and specimen 4028 A (found on a calcareous floor and only slightly ferruginized) were X-rayed together at a distance of 3 feet with 115 kv. for 2 seconds. The skiagram showed that 4029 was far denser than 4028 A, which possibly signifies that it may be more heavily fossilized. The disparity in the skiagrams is also reflected in the Uranium (U_3O_8) content (by courtesy of Dr. K. P. Oakley, British Museum of Natural History), that of 4028 being 14±2 p.p.m. and that of 4029 being 4±2 p.p.m. This indicates that the latter may have come from a higher level, and that conditions for fossilization may have been more favourable. The fluorine contents (by courtesy of Mr. H. E. Krumm of African Metals Corporation, Bellville, Cape) are 1·983% and 1·663% respectively, and the nitrogen contents are 0·11 and 0·085 respectively.

List of Material

		Hopefield No.	*S.A. Museum No.*	
A. GIRAFFA		3345	11716	right P^2
B. SIVATHERIINAE				
(1) *Cranial fragments*		4372 B	11717	base of a skull
		4372	11717	posterior horn-core
		4372 A	11717	fragments belonging to 4372
		4373	11718	posterior horn-core
		4373 A	11718	anterior horn-core
		4373 B, C	11718	fragments belonging to 4373
(2) *Teeth*				
	Upper	4025	11719	right P^3
		4027	11720	right M^1
		4023	11721	left M^2
		4024	11722	left M^3
	Lower	4026	11723	incisor
		4374	11724	left M_1 or M_2
		4028–4028 A	11725	fragment of left mandible with M_2—M_3
		4029—4029 B	11726	fragment of left mandible with M_1—M_3
		4030	11727	right M_2
		4031	11728	right M_3
		4030 A	11727	fragments of roots and pillars

Description

A. Giraffa

3345 (plate 45(*c*), (*d*), (*h*))

This is a right P^2. The tooth is in late wear.

Buccal surface. There is a well-defined cingulum. The surface has a 'W' formation with marked parastyle and metastyle as well as a marked paracone. Between the latter and the two styles there are deep grooves. In anterior or posterior view, the lingual and buccal surfaces slope towards each other in the direction of the apex.

Lingual surface. The enamel is finely rugose and there is a well-marked cingulum. The lingual surface slopes sharply from the cingulum towards the apex in a buccal direction. There is a smooth surface on the posterior aspect of the tooth indicating contact with P^3.

Occlusal surface. The enamel of the paracone is arc-shaped, while the occlusal edge of the lingual surface is more or less straight. The central pit is shallow (because of the marked attrition) and it is slightly curved, the ends pointing towards parastyle and metastyle.

Roots. There are three roots, one lingual and two buccal, the one buccal being broken off at its base, while the other is partly broken. The roots are very short and tend to be triangular in shape.

Diagnosis. Its features and dimensions exclude it from the *Palaeotraginae*, such as *Giraffokeryx* and *Okapia.* The flat profile and slope of the lingual surface of the tooth are uncommon features among *G. camelopardalis* in which a rounded bell-shaped body is the typical shape, but they are observed in *G. gracilis* (Arambourg, 1947, pl. XXII, 1a). The only premolar known to represent *G. gracilis* is a P^4 which is smaller in its overall dimensions than that of *G. camelopardalis.*

Although 3345 falls within the range of *G. camelopardalis* both for A–P and transverse dimensions it tends to be at the lower end of the range. As it is not possible to compare 3345 directly with a *G. gracilis* specimen, it is tentatively assigned to *G. camelopardalis.* This view is strengthened by the fact that the Transverse/A–P index of 3345 is identical to the mean index (123) of P^2 in *G. camelopardalis.* Nevertheless it should be kept in mind that the non-metrical features of the Hopefield specimen are very suggestive of those of the *G. gracilis* premolar. This fact may be more significant than its metrical relationship to *G. camelopardalis* because of the extensive range of variation of the latter (table 7).

B. Sivatheriinae

(1) Cranial fragments

4372 B (plate 42(*a*), (*b*))

Five fragments, found *in situ* associated with the horn-cores 4372, 4373 and 4373 A, were reconstructed to form the base of a skull in the region of the foramen magnum. It contains portions of the two occipital condyles, most of the lower and most of the upper border of the foramen magnum and a portion of the occipital bone. On the inner aspect of the fragment, the bone structure consists of numerous large and small inter-connecting sinuses. The medial edges of the condyles project inwards slightly, decreasing the side-to-side breadth of the foramen magnum. The medial condylar surfaces are not complete, while the lateral articular portions are missing. The medial surfaces are slightly convex from side to side and fairly convex from front to back. There is a small groove on the postero-medial aspect of each condyle where it is continuous with the base of the skull. The striking features of the foramen magnum, viewed from the inferior aspect, are its large size and its almost circular appearance.

The postero-superior border of the foramen magnum forms a broad, flattened arc rather than the acute-angled arch of the modern giraffe. Although a portion of the bone is missing above this region, it is clear that the protuberant mass of solid bone where the two exoccipitals and the supraoccipital fuse in a triradiate fashion, which is present in the modern giraffe, is absent in the fossil specimen. In fact it appears that there is a thickened pillar of bone (the region of the exo-supraoccipital suture junction) leading up to the occipital crest. This feature is very similar to that observed in *Sivatherium giganteum* (see Falconer and Cautley, 1846–9, plate XCII, 1c), except that in the Hopefield specimen the postero-superior border of the foramen magnum appears broader than in *giganteum*. Furthermore, the postero-superior portion of the occipital condyle is angulated quite differently to the foramen magnum than in the modern giraffe in that the plane of this region of the condyle is parallel to the occipital surface, while in the modern giraffe it is almost at 90.° This may indicate that the skull was balanced on the vertebral column at an obtuse angle, rather than the right angle between the vertical axis of the upper cervical vertebrae and the plane of the base of the skull of the modern giraffe. Mechanically this would be in accordance with the short neck of the Sivatheriinae, which probably contained a group of powerful extensor muscles to assist in maintaining the balance of the large skull with its massive, heavy, curving horns.

Measurements	*4372 B* mm.	inches	*Sivatherium giganteum*[1] inches
Minimum intercondylar breadth ..	56·0	2·2	2·6
Foramen magnum:			
Maximum A–P, internal	51	2·0	
Maximum A–P, external	58	2·3	2·3
Maximum breadth, external ..	58	2·3	
Maximum breadth, internal ..	61	2·4	

Table 37

[1] Falconer and Cautley, 1836.

4372 (plate 43)

This is a Sivatherine posterior horn-core (so-called 'antler') which was found to be fairly complete after reconstruction of the fragments. The base is pear-shaped, narrow anteriorly, the posterior part being rather globular. The lower part of the horn-core, as high as the flange, is hollow, narrowing superiorly, and only at the lowest end (for *c.* 12 cm. from the broken edge) is sinus formation visible. The base is fragmented and incomplete, the anterior portion missing and the flange broken off at the anterior border. The body of the horn-core is fairly complete, but the tip is missing.

Just above the base the core turns outwards, and at the base of the second knob it begins to twist posteriorly and laterally, so that the outer surface tends to face anteriorly. The posterior border is rounded; the anterior border at, and above, the flange narrows (and it is more angular than at the base) while nearer the tip, above the second knob, the anterior border becomes rounder.

There are deep longitudinal grooves running up on the medial convex surface. There are three grooves very close together at the base of the flange apparently diverging up from a single point. At the upper end of the flange the posterior groove swings sharply towards the posterior border, while the anterior two slowly separate, and the posterior of these two swings more acutely backwards opposite the second knob. The anterior groove runs up parallel to the anterior border as far as the second knob where it crosses the medial surface posteriorly and upwards towards the tip. In addition, arising from the anterior part of the base, there are three other grooves which travel obliquely upwards (from a point behind that of the above-mentioned grooves) towards the posterior border opposite the middle of the flange, and there they tend to disappear towards the back.

Measurements (mm.):

Circumference at base	*c.* 400	
Circumference between flange and knob 2	*c.* 330	
Circumference 100 mm. above knob 2	*c.* 265	
Circumference at tip	—	
Total length along posterior border	*c.* 590	
	A–P	*Side-to-side*
Base	*c.* 117·0	*c.* 127
Between flange and knob 2	*c.* 130	82·0
Above knob 2 (100 mm.)	91·0	72·0
At tip	—	—

TABLE 38

4373 (plate 44)

A posterior horn-core, the partner of 4372. No additional features are observed on it as it has the same general appearance of 4372. But, viewed from the front, the anterior border has a distinct sinuous ('twisted') appearance (see also Old. 86 (BK II)). It is rather incomplete, especially on the anterior border and convex surface. Therefore, the measurements would all be approximate and as they would add nothing to what has been obtained from 4372, no measurements are given.

4373 A (plate 42(*c*), (*d*))

This is the posterior portion of an anterior horn-core found in association with 4372, 4373. One surface is markedly concave, leading from the base to an irregular rounded knob (cf. C 431 from Orange Free State). No sinuses are visible at the base which is broken away. This is the first Sivatherine anterior horn-core to be described from Africa. Thus it becomes the paratype for *Sivatherium olduvaiense* (see 'Discussion', Section III).

Height of fragment .. 160 mm.
Tip of fragment .. 55 mm. (transverse) × 59 mm. (A–P).

4373 B

A number of small fragments found with 4373 which cannot be fitted into the reconstruction.

4372 a, b, c, etc.

Groups of fragments found in association with 4372. Some are tiny fragments of the horn-core, but there are also a few fragments of skull, too small for identification or description.

(2) TEETH

4025 (plates 45(*a*), (*f*), (*g*); 50(*a*))

This is an isolated tooth, a right P^3.

Buccal surface. There is a rounded cingulum. The posterior half of this surface is missing. The parastyle bulges markedly below the cingulum, while a deep cleft separates the parastyle from the paracone.

Lingual surface. The enamel is fairly rugose and there is a marked rounded cingulum.

Roots. There are three roots. The lingual root which represents the root of the protocone is massive and rounded, and it projects medially. The buccal roots are broken off, but the anterior appears larger than the posterior root.

General shape. The tooth is very large, the buccal surface being flattened, while the lingual surface is arc-shaped. The central pit tends to be U-shaped, its enamel surfaces being widely separated in the centre; the 'arms' of the U taper towards the anterior and posterior ends of the buccal surface. The enamel on the lingual aspect of the pit is evaginated into it posteriorly, and the dentine here contains a rounded cone of enamel (cf. Makapansgat, M 1114). The paracone is wide from side to side, and its dentine tapers both anteriorly and posteriorly.

4027 (plates 46(*a*); 47(*a*); 48(*a*)).

An incomplete isolated right upper molar, probably M^1, in rather advanced wear.

Buccal surface. Marked, rounded cingulum. The tooth is rather fragmented and the paracone is missing. The metacone is similar to that of M^2, 4023 (*vide infra*), and the mesostyle again is prominent.

Lingual surface. The rugosity is finer than in the other teeth. The cingulum is marked and rounded. There is a bulge below the cingulum which is more marked in the anterior than in the posterior pillar. In the posterior pillar, this bulge gives way to a sharp outward angulation of the lingual surface in the direction of the apex, similar to 4024 (*vide infra*). The two pillars meet on the lingual aspect, similarly to those of 4024, i.e. the folding of the two contiguous enamel sides of the pillars being in an anterior direction.

Occlusal surface. The dentine is hollowed out on the 4 cones, forming an arc in a side-to-side direction. The central pits tend to be U-shaped: as in many of the other upper molars, the enamel on the lingual side tends to be U-shaped, while on the buccal side it is V-shaped. The U-shaped side however is more worn than the V-shaped one.

The inner arms of the two pits are not continuous, although the enamel of the two arms are touching each other. As in M^2 (4023), the posterior part of the pit of the anterior pillar has an evagination directed buccally towards the mesostyle.

Roots. The lingual root is broad, thickened above each pillar and a vertical groove on the medial aspect demarcates the two parts. The posterior buccal root tends to be oval in shape and flattened from front to back in an antero-posterior direction. The anterior buccal root is missing.

4023 (plates 46(*b*); 47(*a*); 48(*a*))

An isolated left M^2, found in association with 4024, with which it establishes a contact. The tooth is in a rather advanced stage of wear.

Buccal surface. This is similar to 4024 (*vide infra*) but the mesostyle, which is here complete, is very marked and appears to be associated with the posterior rather than with the anterior pillar. In the central hollow of each pillar there is a slight ridge of enamel (the costa), stretching up from the cingulum towards the apex of the tooth. This is more marked on the anterior pillar. The parastyle is broken off.

Lingual surface. There is a marked cingulum below which there is a slight bulge in each pillar. The enamel is rugose. The enamel is raised in a marked ridge on the anterior aspect of the tooth (protostyle).

Occlusal surface. The anterior pillar is again larger than the posterior one, and both tend to be arc-shaped on the lingual aspect. The slope of the buccal and lingual aspects are similar to those of 4024 in that the lingual surface of the protocone has a more vertical slope than that of the hypocone, while this is reversed on the buccal surface where the metacone is more vertical than the paracone. The central pits are more V-shaped, although the apex of the V, which points lingually, is slightly flattened. The inner arms of the V of each pillar become continuous with each other in the region of the mesostyle. Just on the anterior side of this point the pit of the anterior pillar has a marked evagination, which almost reaches the enamel junction of the two pillars on the lingual aspect.

Roots. They present an identical appearance to those of M³ (4024), but the tip of the lingual root tends to be angulated in a vertical direction, and the lingual root is shorter than the buccal ones. The posterior buccal root is larger than the anterior one; both are triangular in shape. The tips of the anterior and posterior buccal roots curve anteriorly and posteriorly respectively.

4024 (plates 46(*c*); 47(*c*); 48(*c*))

An isolated left M³. It is fairly complete, rather cracked, with most of the buccal roots missing.

Buccal surface. The enamel is rather rugose and not as smooth as in the lower teeth. The cingulum is well marked and rounded but in the centre of each pillar the area just below the cingulum tends to be scooped out. The cingulum becomes continuous with parastyle, mesostyle and metastyle, forming costae, so that viewed occlusally, the surface has a hollowed-out effect between these three costae.

Lingual surface. The enamel is rather rugose. Below the rounded cingulum there is a slight bulge which is more emphasized on the posterior pillar. The enamel is thrown into horizontal ridges on the anterior and posterior surfaces about 5 mm. from the crown-root junction (forming the protostyle and hypostyle respectively). The lingual and buccal surfaces of the tooth tend to slope towards each other in the direction of the apex, as in 4023. On the posterior pillar, there is a marked depression between the hypocone and the metastyle, which tends to accentuate the metastyle. Similarly, there is a depression between paracone and parastyle. This 'pinched' effect emphasizing the metastyle and parastyle is found close to the crown-root junctions and is a common feature in Sivatherines (e.g. F 3655, C 426, MMK 3685). This effect may also be seen on the posterior side of the posterior buccal root (e.g. C 426, 4024). The junction between the anterior and posterior pillars is not marked, the enamel surface of each pillar being contiguous for about 6 mm. towards the centre of the tooth.

Occlusal surface. The shape of the lingual enamel edge of the two pillars is V-shaped, but the posterior is much narrower and smaller, the latter effect being produced by the more acute slope of its lingual surface towards the apex. The central pits are U-shaped, the central portion of the U being fairly wide, while the enamel sides of the 'arms' tend to come close together. The outer arms of each pit curve, one towards the parastyle and the other towards the metastyle, while the two inner arms are directed towards the mesostyle. The mesostyle is missing in part. The central portion of the U in the anterior pillar has a slight evagination posteriorly in a lingual direction. The image of this in the central pit of the posterior pillar is broken.

The tooth (as well as 4023) illustrates very well the typical occlusal wear. The enamel and the dentine are raised in a straight line from side to side in the centre of each pillar, while they are well worn along the anterior aspect of the anterior pillar and the posterior aspect of the posterior pillar. Maximum wear has occurred along the contiguous surfaces of the two pillars.

Roots: The lingual roots of each pillar are fused by a plate, so that in effect one only finds one broad root on the lingual side, with the anterior pillar reflecting the largest bulge on the root. The two buccal roots are separated, but the posterior one is broken off near the base and the anterior root is broken at the crown-root junction. The lingual root is angulated in a medial direction. The buccal roots are arranged so that the posterior root points backwards, and the anterior one forwards and outwards.

4026 (plates 45(*b*), (*e*), (*i*); 50(*b*))

This is an incomplete isolated incisor. Assuming for the purpose of description that it is a right incisor, the anterior half of the crown is broken, mainly on the buccal aspect. The enamel is finely rugose. The enamel on the occlusal edge of the tooth on the buccal aspect is broader than it is at the crown-root junction. Looked at from the side, the 'apron' appearance of the enamel is again observed. On the posterior surface the enamel has a sharp ridge running up from the cingulum to the occlusal surface. The posterior surface on the lingual side of this ridge has no cingulum. Near the occlusal edge this ridge is worn, suggesting contact with a contiguous tooth. The lingual aspect of the tooth has no enamel, indicating that the tooth is in advanced wear, and the dentine is slightly raised at the crown-root junction.

On the buccal aspect, in the centre of the tooth, the enamel presents a groove which extends from the occlusal edge to the bulge above the cingulum.

Measurements of 4026 (*mm.*)

Total height	72+
Crown (buccal) height	34·7
Length (A–P)	*c.* 21
Maximum breadth at the crown-root junction ..	18·4

4374 (plates 46(*d*); 47(*d*); 48(*d*))

An isolated, very fragmented lower left molar, M_1 or M_2, found near 4029, 4029 A and B. It consists of the posterior root, part of the hypoconid and entoconid and a small piece of the protoconid. The tooth is very worn. The buccal enamel is rather rugose, the region of the cingulum is broken away and the lingual surface is also broken. In occlusal aspect, the central pit is visible, rather flattened in shape, with its anterior portion curving towards the metastylid.

Measurements of 4374 (*mm.*)

Buccal height	*c.* 17
Length of the hypoconid ..	*c.* 28

4028 (plates 46(*e*); 47(*e*); 48(*e*))

A fragment of left mandible, containing M_2 and M_3 (4028 A), in advanced wear.

M_3

Buccal aspect. The tooth is hypsodont and the enamel is fairly rugose. The cingulum is marked, more particularly on the posterior pillar and on the talonid; it is more rounded on the buccal than on the lingual side where it is only represented by a faint ridge. At the anterior part of the posterior pillar, the cingulum bulges in the region of the ectostylid.

Similarly on the talonid, at the anterior end of the cingulum, there is a nodular hypostylid. The protoconid tends to be angular on the buccal side, and even presents a slight vertical central ridge, which is not observed on the hypoconid.

Lingual surface. The rugosity is smoothed and even disappears opposite the centre of each pillar where there is a slight bulge (costa). At the base of the crown there is a bulge on each pillar, the posterior pillar having the larger bulge. The bulge on the posterior pillar, which is unusually prominent and extensive, tends to resolve itself in an upward direction in three ill-defined ridges: the posterior ridge travelling in the direction of the entostylid, the central ridge (costa) travelling towards the apex of the tooth, and the anterior ridge in the direction of the metastylid. The enamel of the crown of the anterior pillar and of the talonid is broken off.

About 30 mm. above the cingulum of the posterior pillar, on the lingual surface, the enamel forms a horizontal ridge which extends across the anterior pillar and towards the top of the talonid. There are also a few other irregularities of the enamel giving the appearance of ridges.

The buccal surface of each pillar looked at from the side is vertical, whereas the lingual surface is slightly angulated laterally towards the apex.

Occlusal surface. The protoconid and hypoconid form a triangle, but the apex on the buccal side is an obtuse angle of about 110°. The talonid is large; its occlusal view presents an oval surface, flattened from side to side, and its A–P axis is at an angle of 45° outwards to that of the other two pillars.

The central pit is irregular and flattened from side to side so that in the centre of each pillar the enamel of the two sides of the pits is almost touching. The pit is confined to two pillars and only extends very slightly on the occlusal surface into the talonid. The enamel on the buccal side is fairly regular and wavy, being indented at the junction between the two pillars, whereas the enamel at the lingual side gets broader and evaginates towards the parastylid and also towards the metastylid.

Roots. There are two roots: the anterior pillar having a single root which tends to bulge on both the buccal and lingual sides, these bulges being connected by a short flattened plate. The root tends to be vertical and it is separated by a triangular interval from the root of the posterior pillar.

In the region of the talonid the root is also thickened and continuous with the thickened portion of the posterior pillar by means of a hollowed-out plate, so that in effect one observes one massive root. The tips of the roots tend to curve buccally.

M_2

Buccal surface. There is a cingulum which is not as rounded as in M_3, but on the lingual surface it is slightly more exaggerated than in M_3. Also on the anterior surface of the anterior pillar, the cingulum is well marked. In the region of the ectostylid the cingulum tends to bulge somewhat.

Lingual surface. There is a slight bulge above the base of the posterior pillar, and the resolving upward ridges are similar to those in M_3, but less distinct. The bulge above the cingulum of the anterior pillar is less marked, and is really just a thickening of the cingulum; it appears to lead up to the broken parastylid. Towards the posterior part of the anterior pillar, another ridge (costa) stretches upwards from the cingulum towards the apex of the tooth, and between this ridge and the parastylid there is a slight depression. The enamel forms numerous horizontal ridges.

Occlusal surface. Each pillar has a separated central pit: the pits are only very slightly separated in the region of the metastylid; the posterior one tends to be the more irregular, because each end of its arc sweeps towards the metastylid and the entostylid respectively. The central pit of the anterior pillar broadens out anteriorly. The enamel surfaces of the two pillars sweep in towards each other at a sharper angle, so that they meet in a deep wedge between the two pillars. Once again the protoconid and hypoconid form angular apices on the buccal side; the apex of the posterior pillar being slightly more rounded.

On the occlusal surface of the posterior pillar, the dentine has a shallow pit on the hypoconid. This is probably a post-fossilization artifact.

Looking from the anterior aspect, the crown-root junction presents a horizontal line from the lingual surface towards the buccal, and just near the buccal surface the enamel projects down sharply like an apron. This is the best example of this 'apron' effect which is, in general, better displayed in the lower than in the upper teeth.

Roots. The posterior root is broad when viewed from the posterior aspect and towards the tip it curves posteriorly. The anterior root has a similar appearance, but the tip is shorter and less curved. On both roots, the buccal and lingual surfaces bulge more than the central portion of the root. At the crown-root junction, between the two pillars, an accessory rootlet projects down from the anterior pillar for a short distance. The tip is broken.

4029 (plate 49)

Part of the horizontal ramus of a left mandible with M_3, M_2 (4029 B) and part of the root of M_1. The teeth are in advanced wear.

M_3

Almost complete, deeply stained by ferricrete (see Introduction to Chapter 4).

Buccal surface. It is fairly rugose with a markedly rounded cingulum. The ectoconid is marked and pillariform although broken off just below the occlusal level. Just above the cingulum each pillar is rather rounded. Because of the bulge, that part of the buccal surface above it tends to slope lingually, whereas the lingual surface appears to be at about the same angle as in 4028.

The talonid appears to be angulated to the A–P plane of the pillars, but less than in 4028. It has a rounded appearance because of a large bulge of the crown above the cingulum.

Lingual surface. Rather broken. The cingulum is not rounded and not as pronounced as on the buccal side. The surface presents similar features to 4028.

Occlusal surface. The central pit is very similar to 4028. Despite a greater degree of wear, the central pits of the anterior and posterior pillars are not confluent. The ridges of enamel of each pit lie in contiguity. The buccal enamel of the pillars is arc-shaped rather than triangular.

Roots. Appear to be the same as in 4028.

M_2

Incomplete and rather cracked, but most of the features can be recognized. The general appearance is similar to M_2 of 4028.

Buccal surface. Marked, rounded cingulum with a bulge above it on each pillar. There is an obvious ectostylid.

Lingual surface. The crown-root junction between the pillars appears to be more angulated upwards than in 4028.

Occlusal surface. The central pit of the anterior pillar is small and asymmetrically placed towards the anterior end of the tooth; the central pit of the posterior pillar is very compressed in its anterior half; the posterior half presents a small triangular pit, and is very similar to the same region in M_2 of 4028. Anteriorly the pit does not extend beyond the junction of the anterior and posterior pillars, as it does in 4028. These differences however are probably due to wear. The general shape in occlusal view is the same as in 4028.

Roots. Viewed from the front, the apron effect of the crown-root junction is not as marked as in 4028.

M_1

The posterior root is present. It is broad from side to side, and flattened antero-posteriorly.

Measurements of mandible (*mm.*)

Breadth opposite posterior pillar of M_3 ..	*c.* 37
Breadth opposite posterior pillar of M_2 ..	*c.* 47

4030

This is a fragment of a right M_2, the roots of which are completely absent. Most of the posterior pillar has been reconstructed, while only a small piece of the buccal surface of the anterior pillar remains. Although the tooth was found in a number of fragments, these have been rejoined at only the obvious contact surfaces. Because of the angulation of the fragment, the central pit could be wider which would give the tooth an increased breadth, but it was decided to replace the fragments at their minimum breadth.

Although the tooth is in fairly advanced wear, it is hypsodont. From a rounded cingulum the buccal surface slopes medially at a fairly acute angle, and just near the occlusal edge the surface tends to be more vertical. The lingual surface slopes upwards and laterally from the base, so that the width of the tooth at the crown-root junction is far greater than at the occlusal edge.

Buccal surface. The enamel is rather rugose and the buccal surface is irregular. The posterior surface shows a marked indentation at the crown-root junction. There is a small ectostylid present leading from the rather rounded cingulum of the anterior pillar. There is a small bulge above the cingulum of the anterior pillar.

Lingual surface. Only a small fragment of the entoconid remains, but it can be seen from this that the central costa is flattened; there is a slight groove separating the upper portion of the costa from the fragmented remains of the entostylid.

Occlusal surface. A small portion of the central pit remains. It can be ascertained that the occlusal edge of the buccal surface has a broad U-shape.

4031

This is a fragmented portion of an isolated right M_3 in which the talonid is fairly complete, but only a portion of the posterior pillar remains. Most of the posterior root is present. It is most probable that this tooth and 4030, found near it, belong to the same jaw. The tooth appears to have been in fairly advanced wear. It is markedly hypsodont.

Buccal surface. The talonid is very large, presenting a marked cingulum above which the crown surface is not regular. There is a broad flattened bulge above the cingulum and an indentation (convexity towards the lingual surface) just above this at about two-thirds of the distance up from the crown-root junction. The enamel is rather rugose. The posterior half of the buccal surface of the hypoconid is present and has a round cingulum; the surface of the pillar has two indentations, one just above the cingulum and one at about two-thirds of the height from the cingulum. These abnormalities of the surface of the tooth appear to be a purely local phenomenon (? ecological or dietary variation), because anomalies of the enamel are also observed on Hopefield 4028 and 4029.

Lingual surface. The cingulum is represented only by a thin ridge above which there is a bulge on the talonid, and although most of the lingual surface of the entoconid is missing, sufficient remains to indicate that there is a rounded bulge above the cingulum similar to that in 4028 A.

Specimen	Length: Tooth Max.	Length: Tooth Occl.	Length: Anterior Pillar Occlusal	Length: Posterior Pillar Occlusal	Length: Talonid Occlusal	Breadth: Tooth Max.	Breadth: Tooth Occl.	Breadth: Anterior Pillar Max.	Breadth: Anterior Pillar Occl.	Breadth: Posterior Pillar Max.	Breadth: Posterior Pillar Occl.	Height: Anterior Pillar Lingual	Height: Anterior Pillar Buccal	Height: Posterior Pillar Lingual	Height: Posterior Pillar Buccal	Height: Tooth Height Lingual	Height: Tooth Height Buccal
A Milk																	
*DM*²																	
M 646 ..	21·8	.	.	.	.	15·5	.	.	.	.	.	.	.	.	.	10·0	12·8
M 944 ..	21·7	.	.	.	.	15·9	.	.	.	.	.	.	.	.	.	16·0	13·4
*DM*³																	
M 263 ..	22·0	22·0	.	.	.	20·7	.	.	.	.	.	10·8	11·0	.	.	.	.
M 536 ..	26·0	26·0	.	.	.	22·2	.	.	.	.	.	14·4	14·3	.	.	.	.
*DM*⁴																	
M 263 ..	24·5	24·4	12·2	11·6	.	24·0	.	23·1	15·3	23·0	13·4	13·0	12·5	10·3	15·0	.	.
M 1115 ..	26·1	26·0	10·8	12·5	.	24·7	.	24·7	15·4	24·0	12·9	14·3	15·2	15·4	16·5	.	.
M 535 ..	c. 24	c. 24	12·5	12·3	.	25·2	.	24·9	14·0	22·9	11·0	16·1	16·4	16·0	16·7	.	.
M 533 ..	27·4	27·4	10·0	13·2	.	26·5	.	24·7	13·6	24·6	9·7	15·4	18·3	15·2	17·5	.	.
DM_2																	
M 540 ..	14·5	.	.	.	.	8·6	.	.	.	.	.	.	.	.	.	9·3	9·1
M 939 ..	15·7	15·2	.	.	.	8·4	.	.	.	.	.	.	.	.	.	9·4	8·3
DM_3																	
M 540 ..	21·1	.	.	.	.	12·4	.	.	.	.	.	.	.	.	.	9·0	8·6
M 939 ..	22·3	.	.	.	.	13·7	.	.	.	.	.	.	.	.	.	9·6	10·2
DM_4																	
M 540 ..	34·0	.	9·5	10·1	13·1	17·8	.	.	.	.	.	15·0	14·[illegible]	.	.	.	.
B. Adult																	
*P*²																	
3345 ..	18·9	18·9	.	.	.	23·3	17·9	.	.	.	.	.	.	.	.	8·2	13·5
M 532 ..	21·6	.	.	.	.	28·1	15·7	.	.	.	.	.	.	.	.	17·6	19·3
*P*³																	
M 1114 ..	c. 29	.	.	.	.	29·0	.	.	.	.	.	.	.	.	.	17·3	c. 19
M 531 ..	26·0	26·0	.	.	.	30·5	.	.	.	.	.	.	.	.	.	9·8	11·0
M 264 ..	25·8	25·8	.	.	.	29·7	28·8	.	.	.	.	.	.	.	.	10·7	12·5
*M*¹																	
M 552 ..	28·8	28·3	c. 16	c. 14	.	c. 29	.	.	.	c. 26	15·0	.	29·5	14·2	18·4	.	.
M 551 ..	28·8	28·8	12·8	14·1	.	28·7	.	28·7	14·9	27·2	11·0	22·7	22·1	21·4	22·4	.	.
M 263 ..	29·5	29·4	11·0	15·4	.	32·6	.	32·4	16·1	31·4	12·0	20·7	23·2	20·8	22·1	.	.

M^2																	
M 528 ..	c. 30	c. 30	12·0	15·0	.	c. 33	.	.	.	29·6	23·3	7·6	.	8·8	10·8	.	.
M 550 ..	c. 34	c. 34	16·3	c. 17	.	37·2	.	36·7	30·3	33·8	27·0	11·1	11·0	9·2	9·3	.	.
M^3																	
M 528 ..	c. 26	c. 25	12·1	c. 13	.	c. 26	.	c. 26	.	.	.	8·6	.	6·2	.	.	.
M_2																	
M 1113–942	36·7	35·8	17·2	17·2	.	26·5	.	26·4	18·4	25·3	12·0	27·1	c. 24	28·4	24·8	.	.
M 936 ..	32·8	32·3	14·7	17·0	.	23·1	.	.	.	22·7	23·5	14·3	.	15·9	8·4	.	.
M_3																	
M 938 ..	49·5	38·2	16·6	13·8	7·2	c. 24	.	c. 24	10·0	.	8·9	27·0	.	.	.	.	.

TABLE 39. Measurements of teeth of African fossil *Giraffa* (mm.).
All the specimens are from Makapansgat except 3345 which is from Hopefield.

Specimen	Length					Breadth						Height					
	Tooth		Anterior Pillar	Posterior Pillar	Talonid	Tooth		Anterior Pillar		Posterior Pillar		Anterior Pillar		Posterior Pillar		Tooth Height	
	Max.	*Occl.*	*Occlusal*	*Occlusal*	*Occlusal*	*Max.*	*Occl.*	*Max.*	*Occl.*	*Max.*	*Occl.*	*Lingual*	*Buccal*	*Lingual*	*Buccal*	*Lingual*	*Buccal*
A. Milk																	
*DM*³																	
B¹	41·0	40·8	22·8	18·1	.	32·9	.	31·5	20·0	32·5	18·3	24·2	26·7	21·9	30·2	.	.
M 524 ..	42·7	42·4	18·6	20·3	.	32·7	.	28·8	15·2	32·4	15·6	21·3	24·9	21·8	29·0	.	.
*DM*⁴																	
*B*²	46·7	46·7	19·4	23·8	.	39·7	.	36·7	18·2	39·0	16·5	29·6	35·2	27·9	40·6	.	.
M 937 ..	*c.* 43	*c.* 43	18·6	22·3	.	40·0	.	*c.* 39	18·0	36·0	15·7	*c.* 31	*c.* 30	*c.* 30	33·0	.	.
M 941 ..	*c.* 44	.	*c.* 19	*c.* 22·5	.	*c.* 38	.	.	.	.	.	.	.	.	.	.	.
*DM*₃																	
M 525 ..	33·1	33·0	.	.	.	17·9	.	.	.	.	.	.	18·4	.	18·1	.	.
*DM*₄																	
M 539 B ..	*c.* 55	*c.* 53	17·7	14·8	*c.* 20	24·0	.	20·6	10·9	24·0	13·0	26·2	.	27·0	*c.* 26	.	.
B. Adult																	
*P*³																	
4025 ..	.	*c.* 39	.	.	.	*c.* 44	36·6	.	.	.	.	.	.	.	.	25·5	33·3
F 2989 ..	*c.* 34	*c.* 34	.	.	.	*c.* 43	.	.	.	.	.	.	.	.	.	0	13·0
F 39 (?) ..	.	.	32·5	.	.	.	.	*c.* 40	25·3	.	.	.	*c.* 67	.	.	.	.
*M*¹																	
F 3655 ..	*c.* 38	.	.	.	.	*c.* 47	.	.	.	*c.* 47	*c.* 41	.	.	7·7	8·4	.	.
4027 ..	*c.* 45	.	*c.* 21	*c.* 23	.	54·8	.	.	.	50·6	37·5	22·5	.	20·0	32·9	.	.
C 426D ..	.	.	*c.* 20	.	.	.	.	.	.	.	.	11·0	.	.	.	.	.
*M*²																	
F 3655 ..	46·3	46·3	21·3	19·5	.	48·1	.	47·7	41·8	47·8	37·2	11·5	16·3	9·5	16·2	.	.
F 2993 ..	*c.* 48	.	*c.* 20	*c.* 25	.	*c.* 54	.	.	.	47·2	*c.* 25	29·0	.	*c.* 30	*c.* 43	.	.
4023 ..	*c.* 49	*c.* 49	23·2	21·0	.	47·0	.	*c.* 44	36·2	43·2	31·0	23·1	32·3	20·0	37·4	.	.
C 426B ..	.	.	25·0	*c.* 26	.	.	.	.	.	.	.	.	.	8·6	.	.	.
C 426C ..	.	.	24·8	22·4	.	.	.	.	.	.	.	.	.	11·2	.	.	.
*M*³																	
F 3655 ..	49·5	49·3	20·8	19·7	.	46·0	.	46·0	37·2	40·1	*c.* 32	8·8	18·7	11·0	*c.* 19	.	.
4 BK II ..	44·0	*c.* 44	21·4	18·8	.	*c.* 49	.	*c.* 49	39·7	.	.	13·6	22·1	11·6	.	.	.
109 BK II	51·0	49·1	27·5	22·7	.	50·5	.	50·5	26·3	46·0	*c.* 11	40·6	47·0	*c.* 43	50·0	.	.
4024 ..	53·0	53·0	30·0	20·8	.	46·0	.	42·0	*c.* 34	39·6	28·0	23·5	.	*c.* 23	35·2	.	.
C 426A ..	*c.* 60	*c.* 60	27·5	23·5	.	51·9	.	51·9	*c.* 46	47·7	40·7	9·8	.	7·6	21·6	.	.

MMK3685	53·8	53·6	21·0	24·0	.	54·6	.	54·6	32·9	c. 50	26·3	25·8	c. 34	c. 27	c. 32	.	.
P_2																	
6	26·0	22·8	.	.	.	19·8	17·8	.	.	.	.	.	.	.	.	22·3	21·0
M 553A	c. 26	.	.	.	.	c. 18	.	.	.	.	.	.	.	.	.	c. 21	c. 24
M 553B	c. 26	.	.	.	.	c. 17	.	.	.	.	.	.	.	.	.	c. 22	c. 22
P_3																	
365	34·0	33·5	.	.	.	25·2	23·4	.	.	.	.	.	.	.	.	17·1	17·9
6	36·3	35·8	.	.	.	29·5	27·2	.	.	.	.	.	.	.	.	18·6	19·0
M 553B	c. 36	c. 33	.	.	.	c. 23	.	.	.	.	.	.	.	.	.	c. 35	.
P_4																	
365	37·0	37·0	25·1	10·5	.	28·3	.	28·3	26·2	28·0	25·8	17·1	c. 18	15·7	13·3	.	.
1	41·4	40·6	27·5	11·7	.	28·3	.	27·6	27·6	28·3	26·6	26·3	18·7	20·8	16·4	.	.
6	42·4	42·4	26·0	12·3	.	32·4	.	29·4	29·4	32·4	30·0	28·2	20·8	23·9	16·7	.	.
5	46·0	45·9	31·4	10·2	.	32·0	.	30·8	14·0	32·0	20·5	51·7	50·4	42·3	38·2	.	.
7	47·4	47·4	32·0	.	.	c. 31	.	c. 31	9·8	28·5	15·0	.	.	.	c. 37	.	.
F 2991	40·6	40·6	27·3	10·3	.	31·4	.	28·5	28·5	31·4	31·4	36·3	26·6	30·0	16·0	.	.
2	39·6	38·8	29·0	8·9	.	29·9	.	29·9	c. 27	28·4	29·9	35·0	c. 33	36·0	c. 21	.	.
M_1																	
F 3656	.	.	.	19·0	.	33·2	.	.	.	33·2	30·4	.	.	16·1	15·6	.	.
91	.	.	.	c. 22	.	38·8	.	.	.	38·8	34·6	.	.	.	.	.	.
Nguntiri	c. 47	c. 46	c. 22	22·5	.	32·9	.	32·0	c. 27	32·9	29·7	c. 20	20·1	c. 18	18·3	.	.
365	c. 46	c. 46	21·8	c. 24	.	33·3	.	33·3	32·8	32·7	31·3	9·2	10·2	11·5	15·5	.	.
1	c. 44	c. 44	c. 23	21·6	.	33·2	.	32·6	30·7	33·2	30·2	27·0	24·4	23·7	22·6	.	.
6	44·0	44·0	20·4	21·0	.	39·5	.	33·2	30·8	39·5	36·7	18·8	16·7	18·0	11·4	.	.
M 553B[1]	c. 49	c. 47	c. 22	22·9	.	34·7	.	31·2	c. 22	34·7	c. 21	36+	31·7+	39+	36·6+	.	.
105	47·8	44·8	22·2	22·1	.	27·9	.	27·9	25·0	26·0	23·0	c. 29	23·4	c. 27	.	.	.
132	c. 43	c. 43	c. 22	19·8	.	29·0	27·3	27·3	24·7	29·0	27·0	c. 16	19·2	0	16·0	.	.
8	.	.	23·5	.	.	.	.	32·7	26·6	.	.	35·0	32·0	.	.	.	.
116	c. 47	.	c. 25	c. 23	.	.	.	c. 28	13·0	.	.	c. 54	c. 46	.	.	.	.
M_2																	
F 3656	50·6	50·6	25·5	22·6	.	36·5	.	34·1	29·7	36·5	33·5	26·1	22·7	21·8	16·6	.	.
92	50·2	50·2	26·4	24·1	.	33·7	.	33·7	21·4	33·2	20·6	42·7	c. 35	c. 41	c. 32	.	.
392	52·4	52·4	26·0	25·7	.	35·0	.	33·2	29·6	34·6	31·0	19·4	17·3	22·5	15·0	.	.
91	53·8	53·4	27·4	25·5	.	38·0	.	36·6	.	38·0	30·1	.	26·9	37·7	27·2	.	.
321	c. 51	c. 51	c. 25	23·5	.	36·8	.	c. 36	c. 30	36·8	33·1	28·0	23·2	24·0	17·3	.	.
Nguntiri	48·5	48·0	24·4	23·3	.	33·8	.	33·8	28·4	33·6	27·5	25·1	22·8	c. 27	26·5	.	.
1	48·6	48·6	c. 25	23·9	.	33·6	.	33·6	28·7	c. 34	.	c. 25	26·6	.	27·6	.	.
6	52·8	52·8	27·3	24·8	.	40·2	.	39·8	32·0	40·2	35·0	27·6	20·9	c. 25	20·1	.	.
4028	c. 55	c. 55	c. 28	c. 28	.	.	.	.	.	38·2	31·8	.	.	30·0	31·5	.	.
4029 B	c. 49	c. 49	c. 24	c. 23	.	.	.	.	.	32·3	32·3	.	.	26·1	c. 24	.	.
M 553B[1]	c. 53	c. 52	28·0	22·8	.	33·2	.	33·2	19·1	33·0	18·8	39+	36·2+	41+	33·3+	.	.

Specimen	Length					Breadth						Height					
	Tooth		Anterior Pillar	Posterior Pillar	Talonid	Tooth		Anterior Pillar		Posterior Pillar		Anterior Pillar		Posterior Pillar		Tooth Height	
	Max.	*Occl.*	*Occlusal*	*Occlusal*	*Occlusal*	*Max.*	*Occl.*	*Max.*	*Occl.*	*Max.*	*Occl.*	*Lingual*	*Buccal*	*Lingual*	*Buccal*	*Lingual*	*Buccal*
M 943 ..	.	.	.	24·5	.	.	.	.	.	.	c. 19	.	.	.	49+	.	.
C 1492* ..	.	60·8	.	.	.	.	.	.	19·4	.	24·2	.	.	.	.	.	.
4030 ..	.	.	.	c. 29	.	.	.	.	.	c. 40	c. 26	.	.	.	43·0	.	.
100 ..	.	.	.	.	.	.	.	.	.	.	.	.	.	c. 50	.	.	.
95	c. 50	c. 50	25·5	23·6	.	36·9	.	35·0	25·4	36·9	c. 30	38·0	32·0	c. 29	31·0	.	.
166 ..	50·5	50·5	27·7	22·1	.	33·5	.	30·8	23·9	33·5	c. 26	39·3	39·0	.	c. 35	.	.
																Ratio: *Occl. L. Tal./ Occl. L. Tooth*	
M_3																	
F 3656 ..	68·2	68·0	25·4	21·4	20·0	34·8	.	34·8	28·7	34·0	29·4	28·7	24·3	28·0	24·6	29·4	
92	59·0	58·6	25·0	21·5	12·3	31·7	.	31·7	19·0	30·7	18·5	c. 46	c. 34	49·8	c. 32	21·0	
3	c. 74	c. 69	c. 26	24·5	21·7	c. 31	.	c. 31	c. 27	c. 28	c. 28	.	25·0	.	25·7	31·4	
Nguntiri ..	.	.	22·5	.	.	.	.	c. 31	25·0	.	.	c. 27	24·0	.	.	.	
93	68·7	65·6	23·0	21·4	20·1	32·1	.	32·1	.	30·8	.	0	12·5	0	12·5	30·6	
1	68·2	c. 65	25·0	22·3	17·1	32·1	.	32·1	26·2	30·3	27·6	.	32·7	38·2	29·3	26·2	
4028A ..	c. 77	c. 72	29·0	24·1	c. 18	c. 34	.	c. 34	26·9	32·9	27·2	.	37·8	c. 39	37·3	25·0	
4029 ..	c. 73	c. 71	c. 26	25·5	c. 18	33·8	.	33·8	31·9	31·4	28·4	30·8	26·7	c. 28	28·0	25·4	
6	66·0	66·0	26·2	22·0	17·4	39·7	.	39·7	29·8	36·4	28·4	c. 34	c. 28	38·4	31·3	26·4	
120 ..	63·6	62·1	23·3	19·7	19·1	35·5	.	35·5	31·0	33·3	c. 32·4	26·7	18·6	29·8	18·2	30·7	
4031 ..	.	.	.	.	c. 21	.	.	.	.	c. 33	.	.	.	.	c. 46	27·3	
Marsabit ..	.	.	c. 24	22·4	.	31·5	.	31·5	30·1	29·0	29·0	c. 23	18·5	c. 23	20·6	.	

TABLE 40. Measurements of teeth of Africa Sivatheriinae.

Makapansgat : M 524; M 937; M 941; M 525; M 539B; M 553A; M 553B; M 553B¹; M 943.
O.F.S. : B¹; B²; F 39; C 426A; C 426B; C 426C; C 426D; MMK 3685; C 1492.
Olduvai : F 2989; F 3655; F BK II; F 2993; 109 BK II; 6; 365; 1; 5; 7; F 2991; 2; F 3656; 91; Nguntiri; 105; 132; 8; 116; 92; 392; 321; 100; 95; 166; 3; 93; 120; Marsabit Road.
Hopefield : 4025; 4027; 4023; 4024; 4028; 4028A; 4029; 4029B; 4030; 4031.

Occlusal surface. The occlusal surface is extremely broken but it can be seen that the talonid is angulated slightly to the longitudinal axis of the tooth in a lateral direction. The talonid is large and oval.

4030 A

These are a number of small fragments found in the vicinity of 4030 and 4031, which cannot be included in their structure. They consist of the tips of two lower molar roots and many small fragments of cones.

SECTION III

GENERAL DISCUSSION AND CONCLUSIONS

Sub-order Ruminantia

Family Giraffidae

subfamily Sivatheriinae

Genus Sivatherium Falconer & Cautley 1835–6

(Syn. Indratherium Pilgrim, G. E., 1910. *Rec. Geol. Surv. India*, **40**, pt. 1, 63)

Sivatherium olduvaiense Hopwood 1934*

* Hopwood's specific name is retained, but the masculine form *olduvaiensis* is here corrected to the neuter *olduvaiense*, a form which Hopwood used in 1936 but dropped in 1937.

1934 *Helladotherium olduvaiensis* Hopwood, *Ann. & Mag. Nat. Hist.* (10) *17*, 546.

1936 *Sivatherium olduvaiense* Hopwood, *Ann. & Mag. Nat. Hist.* (10) *17*, 636.

1937 *Sivatherium olduvaiensis* Hopwood. Dietrich, W. O., *Wissensch. Ergebnisse der Oldoway Exped.* 1913. Dr. H. Reck, edit., p. 106.

1942 *Sivatherium olduvaiense* Hopwood. Dietrich, W. O., *Palaeontographica*, *94*, A: 43.

1947 *Griquatherium cingulatum* Haughton. Cooke, H. B. S., & Wells, L. H., *S. Afr. J. Sci.*, *43*, 232.

1948 *Sivatherium olduvaiense* Hopwood. Arambourg, C., *Mission Scientifique de l'Omo* (1932–3). T. *1*, Fasc 3, Paléontologie, Paris, Mus. d'Hist. Nat., p. 376.

1948 *Libytherium maurusium* Pomel. Arambourg, C., *C.R.S. Soc. Géol. France*, Paris, p. 178.

1953 *Sivatherium* sp. Dreyer, T. F., *Res. Nas. Mus.*, Bloemfontein, *1*, pt. 3, p. 74.

Sivatherium olduvaiense vanhoepeni subsp. nov.

1932 *Orangiatherium vanrhyni* van Hoepen, *Pal. Nav. Nas. Mus.*, *2*, pt. 5, 63.

Sivatherium olduvaiense haughtoni subsp. nov.

1949 *Griquatherium haughtoni* Cooke, *Geol. Surv. Mem.* No. 35, pt. 3, 58.

Sivatherium olduvaiense subsp. indet.

Two milk molars from ? Cornelia ? Florisbad. See this paper, p. 526.

Sivatherium cingulatum (Haughton)

1922 *Griquatherium cingulatum* Haughton, *Trans. Geol. Soc. S. Afr.*, *24*, 11.

Genus Libytherium Pomel 1892

1892 *Libytherium maurusium* Pomel, *C.R. Acad. Sci.* (Paris), *115*, 100.

CHAPTER I

SUMMARY OF OBSERVATIONS ON AND VARIATIONS IN SIVATHERINES

A. Cranial Fragments

(1) skull

The only fragment of a skull known from Africa is specimen 4372 B from Hopefield. The predominant features are the great circular size of the foramen magnum, the absence of the supraoccipital bulge and the orientation of the occipital condyles (see page 475).

(2) horn-cores

There are two pairs of horns, the major features of which are:

(*a*) *Anterior horn-cores.* There are two African specimens from which conclusions may be drawn, namely, at Hopefield and at Tierfontein (O.F.S.). The Hopefield specimen is incomplete, but the available fragment corresponds closely to the corresponding region of the Tierfontein specimen. The conclusions are based on the pooling of observations on both specimens. The horn is short, with cranial sinuses projecting slightly into the base. The horn is flattened from side to side, presenting two surfaces and two borders. The anterior border is rounded and has a peculiar cauliflower-like prominence superiorly. The posterior border is also rounded medio-laterally, but from above downwards it presents a concavity facing posteriorly. The one surface is particularly marked by deep grooves, especially near the front. As will be demonstrated in the discussion below, the Hopefield and Tierfontein material are to be referred to *S. olduvaiense.* The Hopefield specimen 4373 A becomes the paratype, because the authors identified it as an anterior horn-core before studying the Tierfontein specimens. Van Hoepen (1932) mentioned only the posterior horn-core definitively, but did not recognize the other specimen (van Hoepen's 'terminal fragment') as an *anterior* horn-core. He also did not indicate that either specimen belonged to the giraffids.

(*b*) *Posterior horn-cores.* Posterior horn-cores have been recovered from North Africa—St. Arnaud (Arambourg, 1948), Aïn Hanech (near St. Arnaud) and Garet Ichkeul (Tunisia) (Arambourg, 1949)—East Africa (Olduvai Gorge), and South Africa (Tierfontein and Hopefield). The features common to all of these are:

(i) Posterior horn-cores are of great length, averaging 640 mm. along the posterior border (range 560–840), and of great size, averaging 390 mm. circumference at the base (range 330–410 mm.) (table 41).

(ii) The base is rounded or pear-shaped and is hollowed out by the cranial sinuses.

	Hopefield 4372	Tierfontein 431	St. Arnaud 1948–1–1	St. Arnaud 1948–1–2	Olduvai M 14955	A.M.N.H. 19774	86 Old. Bk II 1952	1.53 Old.	2.53 Old.	3.53 Old.	SHK II Bk II (Base) S. Old. 1952 *plus* M 14954*b* Old. Bk II S
Total length of fragment											
Outer curve				900			810	950	1010	700	840
Posterior border	590	570	780	660	560		710	840	690	430	580
Circumference											
Base	400	360	390	430			415	400	390	360	330
Between flange and knob 2	330	345	290	300		280	350	410	420	360	350
100 mm. above knob 2 ..	265	258	275	250			330	300	290	310	
At knob 3		255						330	290	360	360
Between knobs 3 and 4 ..							300	280	250	250	270
At tip			137	160				170	170	150	150
A–P diameter											
Base	117	135	110	140			150	159	145	138	117
At base of flange					190		128	154	172	146	
At highest part of flange ..					165						
Between flange and knob 2	130	137	110	115		106	145				
100 mm. above knob 2 ..	91	93	98	92	117		119	105	101	122	
At knob 3		97			88		130	129	104	141	141
At tip			42	55	46		75	52	59	52	49
Side to side											
Base	127	87	98	110			114	127	90		100
At highest part of flange ..					58						
Between flange and knob 2	82	79	70	75		94	89	79	81	77	
100 mm. above knob 2 ..	72	71	65	65	54					70	
At knob 3					53		83	76	75	68	66
At tip			42	45	40		63	52	47	43	46
Flange length				145				267	155		
Internal height of base .. .. (Hollowed by sinuses)			150	150			170		300	130	80
Knob 2, length				90							
Knob 2, base A–P				650							

TABLE 41. Dimensions of posterior horn-cores (mm.) of *Sivatherium olduvaiense*.

(iii) The body of the horn-core is hollow for a varying extent.

(iv) Quite distinct from Cautley's specimen of the 'palmated antler' of *S. giganteum* (Falconer, 1868, I, pl. 21, fig. 3),* the African specimens generally are rounded or oval-shaped. The African specimens present a narrow convex anterior border and a rounded concave posterior border which also has a spiral twist, so that the anterior border becomes superior near the tip and the posterior becomes inferior, i.e. anti-clockwise (right horn) or heteronym (following the terminology of Lydekker, 1913). The horns are characterized by a flange-like projection (which varies in extent) of the anterior border just above the base, and knob-like projections (usually at least three) of varying size along the anterior border above the flange.

It has been clearly demonstrated in Section 1, chapter 7, that in the modern *Giraffa camelopardalis* there are tremendous sex and individual variations within the species. It has been indicated that the previous sub-specific ecological criteria and horn variations are not valid.

There can be no doubt that the dentitions of the *Sivatherium* specimens presently found at Olduvai belong to a single species, *olduvaiense*, in common with those from Hopefield, Port Allan (Tierfontein), Makapansgat, Omo, and Garet Ichkeul. The horn-cores assigned to this species from these sites show a range of variation as wide as that in the modern giraffe. There are degrees of curvature in an antero-posterior direction and also of twisting or torsion. The torsion varies from nothing to almost 90°. This enormous range is found at Olduvai where most of the specimens are curved in an A–P direction with only a slight or medium degree of lateral twist, while a few are twisted markedly so that the planes of the surfaces alter and the horn develops an 'antler' effect. The twist usually occurs just at or above the flange. Unfortunately there are no associations with these horns to indicate the sex of the animals; possibly the males, as in the modern giraffe, show the most marked variations. The few *Sivatherium giganteum* horn fragments found may well be at this extreme range of (? male) variation of torsion, giving a fairly constant 'antler-like' appearance, as described previously.

There are also variations in the number, position and size of the knobs. In some specimens they are evenly distributed along the anterior border. In the horns with marked torsion one or more of the lower knobs get shifted towards the back. The posterior 'branch' or knob on *Sivatherium giganteum* may well again be an extreme example of this. In other specimens the knobs are unevenly distributed, and in a few they tend to be clustered close together near the base of the horn, thus leaving a long smooth anterior border leading up to the tip.

* However, fragment AMNH 19774 (from the Siwaliks), referred by Colbert (1935) to ? *Sivatherium*, is distinctly rounded and is characterized by features observed in the African specimens.

There is no sex dimorphism in the dentition of the modern *Giraffa camelopardalis*. The teeth of *Sivatherium olduvaiense* from each site tend to fall within a single wide range of variation. Based upon the above discussion, it is unreasonable to separate the horn-cores at Olduvai into two species merely because of the fact that some are more markedly twisted than others. The small differences between individuals produce a gradation where the specimens at each end of the range appear to differ fairly widely from each other. But the same, but not correlated, difference can be obtained for the size and the shape of knobs and the A–P curve.

Arambourg (1948) states that *Libytherium* horn-cores differ from other Sivatheriinae, and in particular from the genus *Sivatherium*, because they are not so branched. He refers to the number and size of the knobs, and the torsion of the horns. However, the question of the 'branching' has been discussed above and it, as observed in the African specimens, does not provide a generic or specific criterion of distinction. Furthermore, the North African (St. Arnaud) horn-cores* do not differ essentially from those of the other African Sivatheriinae. In actual fact, it will be demonstrated later in the discussion that for many reasons (one feature being the horn-cores), part of the *Libytherium maurusium* material must be referred to *Sivatherium*.

(v) On the antero-medial convex surface† characteristic and more or less parallel grooves of varying length and depth sweep upwards from the anterior part of the base. The significance of the grooves is not clear. Because of the fact that they appear to radiate from a single point of origin at the base, one gains the impression that they may be of vascular origin (one could compare these with the appearance of the middle meningeal vessels on the interior of a skull). This view had previously been accepted (Abel, 1904; Colbert, 1935; Arambourg, 1948).

However, first, most of the grooves do not decrease in size proportionately to their distance from the origin, which one would expect if they were vessels.

Secondly, one could surmise that a massive horn-core would require a large blood supply, but this argument falls away when one considers that the small anterior horn-cores (about one-quarter of the length and

* These have been studied at the Muséum National d'Histoire Naturelle, Paris, by kind permission of Professors Arambourg and Lehman. The descriptions are not included in this paper as they are to be given by Professor Arambourg in a paper now in preparation. However, he has kindly permitted us to publish the measurements and their general appearance.

† It is extremely difficult to determine to which side a horn-core belongs because of the absence of cranial attachment. However, following careful consideration of the Olduvai specimens 1.53 and 2.53 and of the *S. giganteum* specimens (Falconer & Cautley, 1846–49; Falconer, 1868; Abel, 1904; Colbert, 1935), it has been decided by the authors that the posterior horns are probably directed laterally and backwards, and set at an angle of about 45° to a vertical and horizontal plane, when looked at from the front. In this way, the surface of the horn-core exhibiting the marked grooves becomes the antero-medial surface.

less than one-tenth of the mass of the posterior horn-cores) present equally large or larger grooves. Furthermore, along the line of these grooves, one does not find particularly significant nutrient foramina. In fact the foramina are very small and are found scattered over the whole surface of the horn-core, without any specific relationship to the grooves.

Thirdly, it would appear to be an unnecessary hazard for Nature to have exposed large vessels of great length in such an unprotected region as these curved horns.

The only apparent alternatives are ligamentous or cartilaginous attachments, and on the basis of the large grooves found in other bovids such as *Bubalus* (*Homoioceras*) where cartilage is known to surround the horn-core, it would appear reasonable to assume that these grooves are mainly for cartilaginous attachment, and possibly some of the smaller grooves (those posteriorly) may be for blood-vessels. This is contrary to Colbert's belief (1935) that the Giraffidae never developed a horn sheath during their evolutionary history, and that the hairy horns of the modern giraffe denote a primitive character that typified the various fossil forms.

(3) MANDIBLE

Making use of Makapansgat specimens M 553A, M 553B and M 553B[1], of which A and B[1] belong to the left side, and B to the right side of the same mandible (see Section II, chapter 3), the left half of the mandible was reconstructed by using the mirror image of M 553B. This resulted in a rather robust mandible (fig. 22) which was compared with the Hopefield fragment 4029, the Olduvai specimens 1, 6, 91, 92 and 392, the type specimen of *Libytherium maurusium* (Pomel, 1892) and the North African specimen 1950–1–1 (from Garet Ichkeul, Tunisia; in the Muséum d'Histoire Naturelle, Paris). These were further compared with the juvenile mandible M 539B from Makapansgat, and with data on modern giraffes. From this study the following observations and inferences were made:

(*a*) The total length of the jaw from the anterior alveolar border at symphysis menti to the posterior border of the alveolar socket of M_3 is not much longer in Sivatherines than in modern giraffes (5–15% difference).

(*b*) However, it is in the relative proportions of various significant regions of the mandible that Sivatheriinae differ from *G. camelopardalis*.

(i) The modern giraffe shows an absolute reduction of the length of the premolar-molar series (fig. 24) (for reduction of individual tooth sizes, see 'C. Dentition', *infra*).

The length of the premolar-molar series in proportion to the length of the jaw (as determined above) ranges from approximately 60 per cent in the fossil Sivatherines to 40 per cent in the modern giraffe.

(ii) The distance from the anterior border of P_2 to the posterior border of the symphysis menti is greater in the fossil Sivatherines than in the extant group:

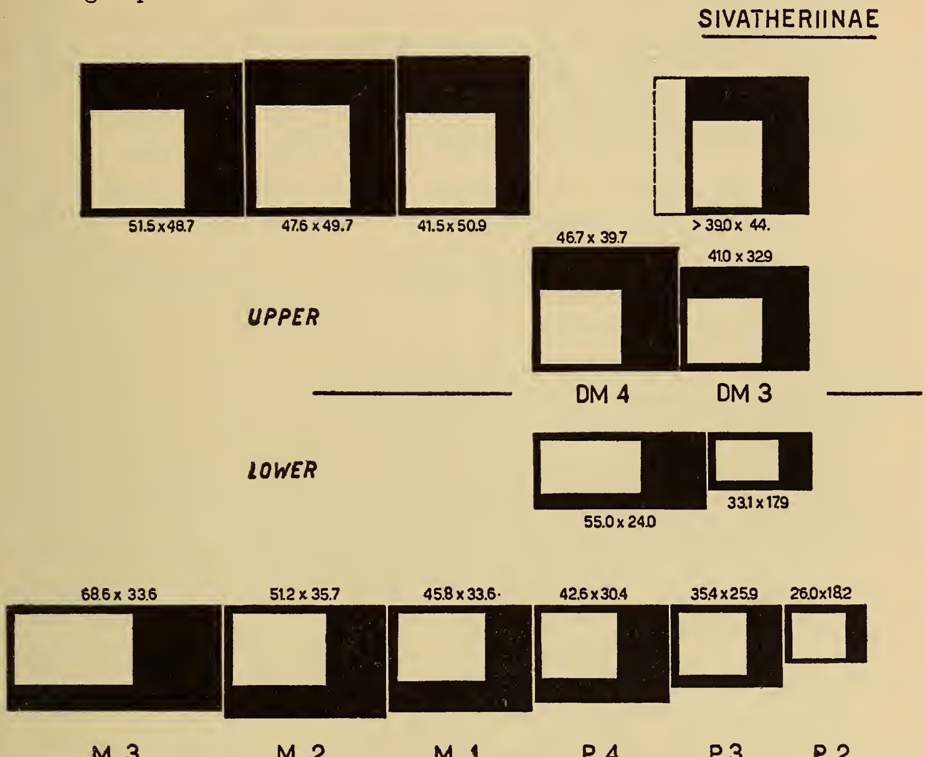

FIG. 24. Graphic representation of the relative ranges of dimensions (A–P and breadth) of adult and milk dentitions in the African Sivatheriinae (excluding F 39, MMK 3685). Mean dimensions are indicated.
Comparable ranges of the modern *Giraffa camelopardalis* are superimposed on those of the Sivatheriinae.

	mm.	*Percentage of total length*
1950–1–1 (North Africa)	*c.* 146	32%
Libytherium maurusium type	*c.* 100	
M 553A	*c.* 103	
G. camelopardalis	*c.* 78	19%

(iii) The distance between the anterior border of P_2 and the posterior border of the foramen mentale is much greater in the modern giraffe:

	mm.
M 553A	99
Libytherium maurusium Pomel—type specimen	100
G. camelopardalis	145

Comparing the data of (ii) with that of (iii) it is clear that foramen mentale is considerably anterior in relation to the position of the posterior border of the symphysis menti in the modern giraffe. In the Sivatherines, the foramen mentale is opposite the posterior border of the symphysis. This is confirmed by direct measurements: in Pomel's specimen of *Libytherium*, they are opposite each other; in Makapansgat 553A, the posterior border of the foramen is *c.* 9 mm. posterior to symphysis menti, while in *G. camelopardalis* this distance is *c.* 67 mm.

(iv) In the modern giraffe, the symphysis menti is considerably longer than that reconstructed in the Makapansgat specimen 553A when the measurement is taken from the position of the tip of the roots of the incisors. The measurements are 152 and approximately 100 mm. respectively.

(v) Following on observation (iv), if, in 553A, one considers the combination of the thickness of the symphysis (41 mm. at the anterior broken extremity; compared with that of *G. camelopardalis* at the same point, viz. *c.* 15 mm.), the shortness of the symphysis and the height of the body of the mandible (*c.* 65 mm.) at the level of the root of I_3, it would seem that the anterior canine-incisor alveolar arch must have been rather cup-shaped in the Makapansgat specimen, so that the teeth would have been embedded more vertically in the jaw than in the modern giraffe. This conclusion is supported by the appearance of the same region in *Hydaspitherium* sp. (A.M.N.H. 19684) (plate 50(*e*)), although it is unlikely that the Makapansgat specimen's teeth were as vertically embedded in the bony alveolus as those of *Hydaspitherium*. The Makapansgat *Sivatherium* canine-incisor row was probably in an intermediate position. Furthermore as the canine has not yet appeared and the canine-incisor arch appears to have 'no space' for it, considerable lateral expansion and increase in depth of the arch would have to take place to accommodate all the teeth. This specimen also indicates that the canine is the last tooth to appear in the dentition, as in the modern giraffe. (See also 'Appendix'.)

(*c*) Certain features concerning the breadth and height of the Sivatherine mandibles are also important:

(i) *Breadth.* The maximal breadth is found in the region between the anterior pillar of M_3 and the anterior pillar of M_1. Anterior to this region, the breadth decreases in a regular progressive fashion. In the juvenile mandible fragment M 539B, the maximal breadth is found opposite the 'talonid' of DM_4. This corresponds to the region opposite P_4 in the adult. If one now compares this with the breadth at this point in the adult, then it appears that a growth increase of about 30 per cent occurs between the two phases.

(ii) *Height.* The maximal height is (as expected) opposite the talonid of M_3, and anterior to this there is a progressive decrease towards the anterior extremity of the jaw. Once again, if one compares the height in the juvenile at a point analogous to that in an adult specimen, then it appears that approximately a 100 per cent increase in growth occurs between the two phases.

(iii) The ratio of height to breadth is expressed as the *index of robusticity*. This is maximal in Sivatheriinae in the region of M_1–P_4, but the range varies tremendously between different specimens (e.g. 48·3 in *Libytherium* (=*Sivatherium*) 1950–1–1; 69·1 in Olduvai 91).

B. Postcranial Fragments

Postcranial fossil giraffid remains from Africa are very scarce. All the material studied by the authors comes from Olduvai.* Further specimens from various sites have been described by:

(*a*) Stromer (1907): a portion of the proximal extremity of a femur, a metacarpal, a fragment of calcaneum showing the fibular facet, and one phalanx: from Wadi Natrun, Egypt.

(*b*) Dietrich (1937): a metacarpal E. 122, from Olduvai gorge; and (1942): from Garussi-Korongo, a metacarpal numbered 1.29, a tibia fragment, a calcaneum, a few first phalanges, astragali numbered Vo 330.1 and Gar.K. 1.29, and 3 cubonaviculare numbered Vo 330.

(*c*) Arambourg (1947): a distal fragment of a scapula from Omo, Ethiopia.

(*d*) Bate (1951): a distal end of a radius and a distal portion of a humerus, from Abu Hugar, Sudan.

The non-metrical features of the Olduvai specimens which are distinctly different from those of extant giraffes, are:

first: in the cubonavicular, the posterior articular facet which articulates with the metatarsal is absent;

secondly, in the metatarsal the vertical anterior groove is much deeper and more scooped out;

thirdly, Arambourg (1947) noted that the spine of the scapula was attached to its dorsum nearer the glenoid cavity;

fourthly, Bate (1951) stated that the breadth of the shaft of humerus and radius relative to the distal end of those bones was much greater in Sivatherines than in the living giraffes.

Comparisons of the measurements of various bones available for study, and of those in the literature, produce a number of interesting features:

1. *Scapula*. There is an overall increase in the size of the scapula (table 42), the maximal breadth at the base showing the most marked differences from

* See also Appendix.

the modern *Giraffa*. There is also a difference in the distance between the root of the spine of the scapula and the glenoid fossa (which has already been noted as a non-metrical feature). It may be noted that the data for *S. giganteum* is very approximate to that of *S. olduvaiense* from Omo.

Measurements[1]	*Helladotherium duvernoyi* Gaudry, 1862	*Sivatherium olduvaiense*[1]	*Sivatherium giganteum* Falconer, 1868	*Giraffa*[1]		*G. camelopardalis*[2]		
				Male	Female	*2128*	*4949*	*4948*
Maximum breadth at the base, including coracoid process ..	150	167		132	126	162	154	151
Breadth at collum	100	116	110	80	75	99	94	83
Length of glenoid fossa	98	102	110–120	88	80	103	90	82
Breadth of glenoid fossa.. ..		80	82–100	78	76	85	83	73
Origin of the spine—glenoid fossa		66		118	114	127	109	132
Breadth of the fossa sub-spinosa, 10 cm. above the glenoid fossa	32	45						

Table 42. Scapula.

[1] After Arambourg, 1947. [2] Musée Royal du Congo Belge, Tervuren.

2. *Humerus*. There is a general similarity in the total length of the humerus of *S. giganteum* and *Giraffa*, although the breadth of the distal extremity and to a less extent of the mid-shaft region is much greater in *Sivatherium* (table 43, page 501).

3. *Radius and Ulna*. The data on the ulna is not sufficient to draw any conclusions (table 44).

	Olduvai *116*	*G. camelopardalis* (S.A. Mus., Cape Town) *17176*
Olecranon process to articular facet, along the superior border	184	143
Maximum height, olecranon process..	117	102
Maximum breadth, olecranon process	78	76
Maximum breadth, articular process	94	87

Table 44. Ulna.

In the case of the radius, although the maximal breadth of the distal extremity in *S. olduvaiense* and *G. camelopardalis* specimens is similar, a short distance above the distal end the breadth dimension indicates that in *G. camelopardalis* the shaft tapers very rapidly towards the middle of the shaft, while in *S. olduvaiense* the bone generally remains wide. There is very little difference in total length between *S. giganteum* (B.M. 39534) and *G. camelopardalis*, but the other Sivatherines appear to have a slightly shorter radius (table 45, page 502).

	? *Sivatherium olduvaiense* Abu Hugar (1)	*Sivatherium giganteum* (3)	*Giraffa camelopardalis* (2)	(3)	17176 S.A. Mus., Cape Town	2128 (4)	4949 (4)	6342 (4)	4948 (4)	4947 (4)
Diameter, articular surface of head ..		132–140				111–125	110–111	103–106	90–119	103–126
Total length		513		465	538	543	497	438	461	517
Proximal extremity: A–P		198				180	175	157	152	165
breadth		213				153	156	129	143	148
Mid-shaft: A–P		85		66	55	79	85	57	69	72
breadth		96		61	51	72	76	63	65	61
Shaft breadth, 'a short distance above distal extremity'	152		137		110	112	99	74	79	103
Distal extremity: condylar breadth ..	130		130		140	122	118	103	111	116
maximum breadth ..		183				139	141	122	127	141

TABLE 43. Humerus.

(1) Bate 1951. (2) id. (3) Our data from U.S.A. Museums. (4) Musée Royal du Congo Belge, Tervuren.

	Old. 115	*Helladotherium* (1)	*Hydaspitherium* A.M. 19770 (2)	*Sivatherium olduvaiense* Abu Hugar (3)	*Giraffa camelopardalis* (3)	(4)	(5) 2128	4949	6342	4948	4947	17176 (6)
Proximal extremity												
Maximum breadth		143					143	136	124	128	135	154
Mid-shaft												
A–P						47	57	53	45	50	52	54
Breadth		74				62	75	69	60	64	67	83
Circumference		270					203	205		188	205	
Distal extremity												
Maximum breadth (at radial tuberosity) ..	122	130	115	140	105		148	129	115	116	130	136
Maximum A–P length	82						101	88	72	82	85	97
Shaft breadth 'a short distance above distal end' ..				135	87		91	93	80	80	90	94
Maximum breadth of proximal end of fragment ..	135											
Length without ulna						755	846	810	710	730	836	
Total length		592	c. 500				989	926	800	831	939	838

TABLE 45. Radius.

(1) Bohlin, 1926 (mean of 3 specimens). (2) Colbert, 1935. (3) Bate, 1951. (4) Our data from American Museums. (5) Musée Royal du Congo Belge, Tervuren. (6) S.A. Museum, Cape Town.

	Sivatherium giganteum B.M. 39.533	Old. 114	AM 19460 *Hydaspitherium* or *Bramatherium* (1)	AM 19460 *Hydaspitherium* or *Bramatherium* (1)	AM 29820 *Hydaspitherium* or *Bramatherium* (1)	*Helladotherium duvernoyi* (2)	*Sivatherium olduvaiense* Garussi Korongo (3)	*Sivatherium olduvaiense* E. 122 (3)	*Sivatherium giganteum* (3)	? *Libytherium* (4)	*Giraffa camelopardalis* (5)	*Giraffa camelopardalis* S.A. Museum, Cape Town (17176)	*Giraffa camelopardalis* 2128 (6)	*Giraffa camelopardalis* 4949(6)	*Giraffa camelopardalis* 6342 (6)	*Giraffa camelopardalis* 4947 (6)
Proximal extremity																
Breadth			95	103	96	109		114	119	108		115	108	102	88	94
Superior articular surface: breadth	120												72			
Superior articular surface: A–P	69												72	66	58	62
Mid-shaft																
Breadth			58	61	56			70		55	48	59	60	53	46	49
A–P										40	47	62	58	56	46	48
Shaft about 60 mm. above distal extremity: breadth		79										87	78	61	52	62
Shaft about 60 mm. above distal extremity: A–P		42										58	53	45	38	43
Distal extremity																
Maximum breadth across condyles		105	100	98	96	100	118	111	119			114	116	102	89	93
Maximum breadth, lateral condyles (anteriorly)		51											49	48	42	44
Maximum breadth, medial condyles (anteriorly)	55	52					55	53	56				49	48	42	44
Breadth, inferior articular surface	120												103			
A–P length of condyles	55	54										75	69	65	57	63
Total length of metacarpal	355		432	398	427	420		290	348	360	659	757	760	744	657	666

TABLE 46. Metacarpal.

(1) Colbert, 1935.
(2) Gaudry, 1862.
(3) Dietrich, 1942.
(4) Stromer, 1907.
(5) Our data from U.S.A. Museums.
(6) Musée Royal du Congo Belge, Tervuren.

Note: AM 19460 are two left metacarpals with the same number.

	Old. 100	BM 39545 *Sivatherium giganteum*	BM 39546 *Sivatherium giganteum*	BM 39547 *Sivatherium giganteum*	*Giraffa camelopardalis* (1)	17176 S.A. Museum, Cape Town	2128 (2)	4949 (2)	6342 (2)	4948 (2)	4947 (2)
Proximal extremity											
Breadth including trochanter		190					183	177		166	176
Antero-posterior diameter of greater trochanter ..		102					94	81		66	67
Antero-posterior diameter of articular surface of head		76					73	71	61	64	67
Transverse diameter of articular surface of head ..		96					94	85	63	79	83
Mid-shaft: A–P					60	71	70	67	61	64	65
Transverse					51	72	57	58	49	54	55
Distal extremity											
Maximum breadth across condyles	161		162	193		171	154	142	132	136	143
Maximum breadth across medial condyle	72					76	72	67	60	67	70
Maximum breadth across lateral condyle	55					76	55	59	42	56	54
Maximum breadth across patellar condyle	78		74				84	85	80	79	83
Cord length of patellar condyle in the centre ..	109		104	119			95	95	84	88	86
Antero-posterior diameter: internally			218				209	202	185	185	200
externally			152				147	143	132	139	147
Total length of femur					492	539	590	539	485	492	550

TABLE 47. Femur.

(1) Our data collected at U.S.A. Museums. (2) Musée Royal du Congo Belge, Tervuren.

	Sivatherium giganteum							*Giraffa camelopardalis*						
	Old. 101	Old. 112	B.M.* 17072	B.M. 18482	B.M. 16611	B.M. 39548	B.M. 39549	(1)	17176 S.A. Museum, Cape Town	2128 (2)	4949 (2)	6342 (2)	4948 (2)	4947 (2)
Proximal extremity														
Maximum breadth ..			152	172	180					169	155	143	142	150
Maximum A–P			89	96	102					109	89	85	88	91
Mid-shaft														
Maximum breadth ..			69					62	81	80	73	63	68	69
Maximum A–P			48					49	62	62	65	42	54	56
Shaft 80 mm. above distal end:														
breadth	87								87	82	69	66	78	74
A–P	64								38	50	49	44	48	49
Distal extremity														
Maximum breadth ..	120	109	117			127	127		126	121	110	102	104	108
Maximum A–P	83	83	82			76	66		86	83	75	75	75	73
Total length			525					572	653	680	648	579	606	684

TABLE 48. Tibia.

* B.M. denotes British Museum (Nat. Hist.). (1) Our data from U.S.A. Museums. (2) Musée Royal du Congo Belge, Tervuren.

4. *Metacarpal.* There is a marked difference in length between the African Sivatherines and *G. camelopardalis,* the Sivatherines being 40–50 per cent shorter, and this also applies to other *Sivatheriinae.* It is here considered that the marked reduction in forelimb length in comparison with the modern giraffe previously noted, is mainly accounted for by the shortness of the metacarpal (table 46).

5. *Femur.* The available information indicates no marked difference between the extant giraffe and the extinct giraffid specimens. Unfortunately no information is available on the total length of the femur of the extinct genus (table 47).

6. *Tibia.* In only one Sivatherine (B.M. 17072) could the total length be measured, and it is approximately 10 per cent shorter than in the modern giraffe. No definite conclusion can be based upon this single observation. However the A–P length and the breadth are approximately the same in the two groups (table 48).

7. *Astragalus* (talus): The *Sivatheriinae* specimens have a much greater proximo-distal length, although the breadth is approximately the same. This increased length of the articular surface of the astragalus (table 49) may have been advantageous to the extinct short-legged animal for its efficient function, that is, to flex and to extend more powerfully for greater speed. It may also have been advantageous for more efficient weight-bearing.

	Sivatherium olduvaiense				*Hydaspitherium* or *Bramatherium* A.M. 19831[2]	*Sivatherium giganteum* BM 16.998	*Giraffa camelopardalis*	
	Old. 102	Old. 107	Vo. 330.1[1]	Ga.K. 39.1[1]			4949[3]	S.A. Museum, Cape Town 17176
Maximum proximo-distal length	113	112	130	112		124	99	93
A–P maximum length, medially	73	71					63	
A–P maximum length, laterally	64	63					60	
Maximum breadth, proximally . .	87	86			65	86	73	81
Maximum breadth, distally . .	*c.* 75	76					72	
Maximum articular breadth, proximally	74	73						
Maximum articular breadth, distally	*c.* 75	76	91	76				

TABLE 49. Astragalus.

[1] Dietrich, 1942. [2] Colbert, 1935. [3] Musée Royal du Congo Belge, Tervuren.

8. *Calcaneum.* No difference is noted between the extant giraffe and the extinct forms (table 50).

	Old. 103	Old. 108	A.M. 19831 *Hydaspitherium* or *Bramatherium*[1]	*Libytherium* Garet el Mulúk[2]	B.M. 39543 *Sivatherium giganteum*	4949 Tervuren[3]	17176 S.A. Mus., Cape Town
Maximum length	216	198	183			202	221
Maximum breadth	69	67			73	54	64
Maximum height, A–P tuberosity ..	69	c. 62			72	62	72
Maximum length, A–P opposite the fibular facet	89	91					
Body length from the superior border of the astragalus facet	131	c. 119				119	133
Minimum body breadth	39	42				31	42
A–P length of fibular facet (on its convex portion)	39	33		40		31	
Breadth of fibular facet	28	24		25		26	
Projection of heel					157		

TABLE 50. Calcaneum.

[1] Colbert, 1935.
[2] Stromer, 1907: ? *Libytherium* discovered in Garet el Mulúk; fibular articulation of a right calcaneum.
[3] Musée Royal du Congo Belge, Tervuren.

9. *Metatarsal.* As in the metacarpal, there is a tremendous reduction in the length of the metatarsal as compared with *G. camelopardalis.* In all other aspects, this bone of the Sivatherines is similar to that of the modern giraffe (table 51, page 508).

10. *Other tarsal and carpal bones.* From the data available no distinct differences may be observed between Sivatheriinae and *Giraffa* (tables 52, 53, 54).

	Olduvai 341
Maximum length	75
Maximum breadth	70
Maximum postero-lateral thickness ..	39

TABLE 52. *Os magnum.*

												Giraffa camelopardalis					
	Old. 106	Old. 111	Old. 314	? *Libytherium* (4)	*Sivatherium giganteum* (1)	*Helladotherium* (2)	AM 19831 *Hydaspitherium* or *Bramatherium* (3)	AM 19688 *Hydaspitherium* or *Bramatherium* (3)	AM 1977 *Hydaspitherium* or *Bramatherium* (3)	AM 19464 *Hydaspitherium* or *Bramatherium* (3)	South African Museum, Cape Town	(5)	2128 (6)	4949 (6)	6342 (6)	4948 (6)	4947 (6)
Proximal extremity																	
A–P length, articular surface	81	84	.	.	94	86	.	.	.	.	94	.	77	83	75	69	73
Breadth, articular surface	93	95	.	88	96	86	78	82	81	68	101	.	89	85	73	72	79
Maximum A–P, medial articular surface	59	59	.	.	.	.	.	.	.	.	.	.	71	61	43	56	56
Maximum A–P, lateral articular surface	64	58	.	.	.	.	.	.	.	.	.	.	72	65	50	61	65
Maximum breadth across centre, medial articular surface	33	36	.	.	.	.	.	.	.	.	.	.	29	23	26	23	25
Maximum breadth across centre, lateral articular surface	40	*c.* 50	.	.	.	.	.	.	.	.	.	.	34	27	28	25	27
Shaft 60 mm. below proximal extremity																	
A–P length	67	65	.	.	.	.	.	.	.	.	77	.	65	63	52	57	65
Transverse breadth	65	72	.	.	.	.	.	.	.	.	65	.	57	59	50	51	54
Mid-shaft																	
Circumference	.	.	.	.	.	194	.	.	.	.	.	.	196	177	—	166	230
A–P length	.	.	.	.	.	.	.	.	.	.	61	46	61	55	50	48	50
Breadth	.	.	.	52	.	.	43	52	48	36	60	45	54	51	53	47	48
120 mm. above distal extremity																	
Maximum breadth	.	.	67	.	.	.	.	.	.	.	.	.	65	56	47	49	55
Maximum A–P	.	.	*c.* 60	.	.	.	.	.	.	.	.	.	48	44	38	41	44
Distal extremity																	
Maximum breadth, trochlea	.	.	109	.	.	.	83	89	89	72	100	.	90	89	81	85	87
Breadth, lateral trochlea	.	.	52	.	.	.	.	.	.	.	.	.	40	43	36	40	40
Breadth, medial trochlea	.	.	53	.	.	.	.	.	.	.	.	.	40	40	34	39	40
A–P length across trochlea laterally	.	.	63	.	.	.	.	.	.	.	.	.	62	58	52	56	58
A–P length across trochlea medially	.	.	61	.	.	.	.	.	.	.	69	.	60	57	51	56	57
Total length	.	.	.	355	415	446	434	431	450	369	802	670	775	760	662	700	785

TABLE 51. Metacarpal.

(1) Dietrich, 1942. (3) Colbert, 1935. (5) Our data from U.S.A. Museums.
(2) Bohlin, 1928. (4) Stromer, 1907. (6) Musée Royal du Congo Belge, Tervuren.

	Old. 104	Old. 110	Old. 109	Vo 330 ? *S. olduvaiense*[1]	Vo 330 ? *S. olduvaiense*[1]	Vo 330 ? *S. olduvaiense*[1]	BM 39844 *Sivatherium giganteum*	17176 S.A. Museum, Cape Town *Giraffa camelopardalis*	4949[2] *Giraffa camelopardalis*
Maximum breadth (side to side) across centre ..	110	108	109	115	120	125	123	109	96
Maximum A–P length across tuberosity of navicular ..	106	106	95				127	98	98
Maximum length of navicular articular facet for cuneiform	55	55	50						69
Maximum breadth *idem* ..	37	37	35				38		31
Maximum length of cuboid facet for metatarsal ..	61	61	55						62
Maximum breadth *idem* ..	45	48	42				46		38

TABLE 53. Cubonaviculare (Scaphocuboid).
[1] Dietrich, 1942. [2] Musée Royal du Congo Belge, Tervuren.

	Olduvai 105	*Olduvai 110 A*
Maximum A–P length	68	59
Maximum breadth (side to side) ..	41	40
Maximum postero-lateral thickness ..	23	23

TABLE 54. Cuneiform.

C. DENTITION

A large series of teeth provides ample opportunity for determining typical features and variations of specimens from a particular site, and also for determining comparisons between dentitions from different sites. The characteristics of the Sivatheriinae teeth studied are:

I. NON-METRICAL FEATURES

(*a*) *Wear.* Those teeth which are either unworn or in the early stages of wear provide evidence that the teeth of the lower jaw are hypsodont, while the teeth up the upper jaw are, in general, at most mesodont, although F 39 is hypsodont. As in all other palaeontological studies on dentitions, the appearance of the various stages of wear may be most misleading if one has not had the unworn teeth available. In the Sivatherine dentition particularly, because of the great breadth of the tooth near the crown-root junction and consequently because of the varying amount of dentine present, and because of the fusion of the cones at different stages, the diagnosis of the teeth must be approached with caution. The large collection of Sivatherine teeth assembled from various sites made it possible to establish a range of the stages of wear of the upper and lower dentition from the unworn teeth to teeth worn right down to the crown-root junction.

(*b*) *Slope and bulge of tooth surfaces.* Another important factor which requires careful consideration is that of the various degrees of slope of the buccal and lingual surfaces of the teeth from the crown-root junction towards the occlusal aspect. Furthermore, in relation to this slope, it has been observed that the profile of the enamel surface of the tooth may be either straight or it may have a rounded bulge in the region of the crown-root junction, quite apart from the cingulum. These variations are not only observed in teeth from the same site, but there may be variations in teeth of the same jaw. These features are seen particularly on the proto-hypocone (-id) enamel surface of the teeth.

In Old. 1, for example, the profile of the buccal surface on the posterior pillar of M_3 tends to be vertical and flat, while in the talonid it has a rounded bulge. Similar rounded bulges are observed in M_1 and P_4. Maximal bulging on the buccal surface is observed on the molars of Old. 6 and Hopefield 4029 (M_3). On the other hand, Hopefield 4028 tends to show a flattened vertical buccal surface, while another variation of the flattened effect is observed in M 553 B^1 where the profile is flat, but it is also sloping in a lingual direction towards the occlusal surface. The same effect is seen in Hopefield 4030. In the opposite direction, Old. 92 shows a very slight bulge above the cingulum, while most of the rest of the buccal surface is recurved so that a slight concavity faces buccally.

Similar variations in the slope and bulging of the enamel on the lingual surface are seen in the upper teeth, except that, where the surface tends to be straight, it slopes in a buccal direction and is not vertical. For example, Old. 109 has a slight irregularity of the enamel just below the cingulum, and the lingual surface slopes buccalwards towards the occlusal surface. In Hopefield 4023 there is a slight bulge below the cingulum and the lingual surface has a slight concavity as it slopes towards the occlusal plane. In Hopefield 4024, there is a rounded bulge below the cingulum and on the posterior pillar the concavity is quite marked. The maximum degree of this is seen in MMK 3685 where, immediately below the prominent cingulum, the lingual surface slopes at an acute angle markedly towards the occlusal surface in a buccal direction and also has a slight concavity facing towards the lingual side.

Specimen F 39 (of the Vaal River site) slopes at a marked angle from the cingulum towards the apex with a slight convexity lingualwards, but just beyond half-way towards the present occlusal edge, the surface tends to become slightly more vertical. It has been mentioned that the entire interior of the tooth is completely filled with breccia, and on radiographic examination vertical fracture lines can be seen, apparently being caused and filled by compressing breccia. This could be an explanation for some of the excessive bulging of the upper part of the lingual surface of the tooth. However, there are no distinct cracks on the surface of the enamel, except for a small one on the anterior edge of the cingulum, and for some small cracks on the occlusal surface. This explanation is only a tentative one, and has not been used as a diagnostic criterion for discussion.

(*c*) *Central pit.* The variations observed in various teeth are purely due to the different degrees of wear and should be regarded as individual variations rather than in the light of taxonomical differences. Similar shapes and variations have been observed in specimens from all the sites in Africa.

(*d*) *Enamel.* The characteristic features and variations of the enamel of the Sivatherine dentition may be described as follows:

(i) *Rugosity*

As already mentioned, in the whole family of giraffids the enamel is rugose, and in the Sivatherines the rugosity is as variable as in other genera, namely from a fine pattern to a gross appearance. These variations are observed in the same specimen or in different specimens from the same site. Old. 6 for instance is finely rugose, while Old. 1 (from the same BK II locality) shows a coarse rugosity. Hopefield 4027 is finely rugose, while Hopefield 4023 (of the same jaw) is coarsely rugose. However, in the Sivatherine teeth in general, the enamel is thrown into far more numerous, closer-packed, vertical 'ridges' (each of which consists of a number of overlapping vertical spikes) than in *G. camelopardalis*, so that they tend to have a rougher appearance of the enamel than the modern giraffe. Even when the authors have described teeth as having a 'fine rugosity', the ridges—although less prominent—were still numerous and closely packed, quite distinct from the modern *Giraffa*, where they are fewer, shorter and separated from each other. The enamel pattern of the African fossil teeth is more akin to *S. giganteum* than the available examples of the other Sivatheriinae, in that in the latter the individual 'ridges' are less spiked.

(ii) *Cingulum*

A cingulum is practically always present on the buccal and lingual surfaces, varying from a thin, linear ridge to a rolled edge. The latter is usually found, when present, on the proto-hypocone (-id) aspect, while the former is typically found on the other aspect of the tooth. On the anterior and posterior surfaces, the cingulum is usually absent or deficient. Furthermore, there may or may not be a bulge related to the cingulum. On the other hand, just above (in lower) or just below it (in upper teeth) there may even be a concavity of the tooth surface (*vide supra*, (*b*)).

(iii) *Styles*

Elevations of the cingulum are commonly present in the form of interpillaric styles (entostyles and ectostylids), but this varies from tooth to tooth and jaw to jaw. The recording of the presence or absence of the styles may be difficult because of the late stage of wear. Indeed, the styles vary in that they may or may not reach the crown-root junction. When they do not, they are usually present near the occlusal aspect of the tooth, so that in late wear the tooth presents the appearance of not possessing that particular style. This inference is drawn from the presence of the style on the unworn teeth.

The median costa is better developed on the anterior than on the posterior pillar, and in the lower teeth it seldom reaches the cingulum, occasionally ending as a rounded bulge above the cingulum. This effect is noticed in teeth from all the sites. The base of the metastylid usually commences about half-way up from the crown-root junction; consequently in late wear of the lower teeth, with the 'absence' of metastylid and median costa, the lingual surface of the tooth presents a rather flattened appearance. The mesostyle is always present as a persistent, well-marked, rounded ridge extending from the occlusal edge to the cingulum. The parastylid is usually ridged and slanting, being continuous at its base with the cingulum. The parastyle is always rounded, prominent and vertical, with its base continuous with the cingulum where it forms a bulge, and its apex tapering off to a point beyond the midpoint of the tooth. The entostylid is usually poorly represented, if present. However, the metastyle presents a fairly prominent bulge in the region of the cingulum, but it is relatively much smaller than the mesostyle or parastyle.

In comparison with the modern (brachydont) *G. camelopardalis*, the African Sivatheriinae show marked differences in respect of the relationship of the styles (-ids) to each other on the buccal (upper) and lingual (lower) aspects of the tooth. In the modern specimens, on the buccal aspect of the anterior pillars of the upper jaw, the parastyle meets the ridge-like prominent costa at an acute angle at its base. Posterior to the median costa the cingulum runs horizontal to the base of the prominent mesostyle. Posterior to the mesostyle, the buccal surface of the tooth is flattened and seldom presents a visible median costa or a metastyle. Consequently, the appearance of the buccal aspect of the upper tooth is that of an inverted trident.

In the lower teeth, each pillar presents a similar appearance, the anterior overlapping the posterior, the median costa being rather rounded, not only in an A–P convexity but also in a superior-inferior convexity, so that the occlusal tip of the metaconid and entoconid tend to bend over in a buccal direction. Behind each median costa there is a slight groove separating it from its respective stylid which is continuous with it about half-way up from the crown-root junction. Below that level, the lingual surface presents a rather continuous smooth bulging appearance.

In the Sivatheriinae, the styles and costae of the buccal surface of the upper teeth tend to be rather parallel to each other, the meeting of the base of the styles with the cingulum being in a broad U-shaped fashion. In the lower dentition, as mentioned above, the entostylids are poorly marked and the parastylids are prominent, which is the reverse of the situation in modern giraffes. Because the parastylid reaches the cingulum near the base of the median costa, the lingual surface has a rather scalloped appearance and is not unlike the general appearance of the buccal aspect of the modern upper teeth.

(*e*) *Orientation.* In the Sivatheriinae, the lingual (lower) and buccal (upper) surfaces of the pillars present a generally smoother, flatter plane than those of the modern giraffes, because the surfaces of the Sivatherine pillars tend to lie more parallel to the longitudinal axis of the jaws than in the modern *Giraffa*, where the surfaces of successive pillars tend to overlap each other more acutely so that each pillar has the appearance of being independent of the next.

The talonid of the lower M_3 tends to be set at a variable angle to the longitudinal axis of the tooth: the axis of the talonid is nearly in line with that of the tooth (180°) in Old. 1, 3, 92, 120, Hopefield 4029, or at an angle of about 130° in Olduvai 6, F. 3656, Hopefield 4028A.

2. METRICAL FEATURES

Tooth	A–P			Transverse			Index		
	N	*M*	*Range of variation*	*N*	*M*	*Range of variation*	*N*	*M*	*Range of variation*
DM^3	1	41·0		1	32·9		1	80·2	
DM^4	1	46·7		1	39·7		1	85·0	
P^3				1	*44·*				
M^1	2	41·5	*38·* –*45·*	2	50·9	*47·* –54·8	2	122·5	121·6–123·5
M^2	3	47·6	46·3–*49·*	3	49·7	47·0–*54·*	3	104·1	96·1–112·4
M^3	5	51·5	44·0–*60·*	5	48·7	46·0–51·9	5	95·0	85·3–111·1
DM_3	1	33·1		1	17·9		1	54·1	
DM_4	1	55·0		1	24·0		1	43·7	
P_2	3	26·0		3	18·2	*17·*–19·8	3	70·2	65·4–76·2
P_3	3	35·4	34·0–36·3	3	25·9	*23·*–29·5	3	73·1	64·0–81·3
P_4	8	42·6	37·0–47·4	7	30·4	28·3–32·4	7	72·7	65·5–77·3
M_1	7	45·8	*44·* –*49·*	9	33·6	27·9–39·5	7	72·0	58·4–89·7
M_2	12	51·2	48·6–*55·*	10	35·7	33·2–40·2	10	70·0	62·8–76·0
M_3	9	68·6	59·0–*77·*	10	33·6	*31·* –39·7	9	49·6	41·9–60·1
I?	1	*21·*		1	18·4		1	87·6	
I?	2	22·3	22·0–22·7	2	17·5	17·4–17·6	2	88·3	76·6–80·0

TABLE 55. Transverse / A–P Index in the Sivatheriinae. The data exclude the dimensions of F.39, MMK 3685 and those teeth not definitely diagnosed as either M^2 or M^3.

(Italicized figures indicate approximations.)

The absolute A–P and transverse dimensions (table 55) in the Sivatheriinae are greatly in excess of those for modern *G. camelopardalis*. The calculation of the Transverse/A–P Index in both cases produces interesting observations:

(*a*) The African Sivatheriinae have a constantly (except for M^1) smaller Transverse/A–P Index than *G. camelopardalis* for the milk and the adult, in both upper and lower, dentitions. This indicates that the A–P length is relatively more reduced than the transverse breadth in the modern giraffe (fig. 24).

Tooth	Series	Upper		Lower	
		Mean	*Range of variation*	*Mean*	*Range of variation*
DM3	*Giraffa camelopardalis*[1]	86·9	78·8– 96·0	66·6	52·6– 78·2
	African Sivatheriinae[2]	80·2		54·1	
DM4	*Giraffa camelopardalis*	92·3	82·0–101·0	52·3	46·2– 58·0
	African Sivatheriinae	85·0		43·7	
P2	*Giraffa camelopardalis*	122·9	104·0–149·0	87·4	56·5–124·0
	Sivatherium olduvaiense[3]	110·0	100·0–119·0	78·0	
	African Sivatheriinae			70·2	
	Sivatherium giganteum[4]	113·0			65·4– 76·2
P3	*Giraffa camelopardalis*	125·1	101·0–157·0	91·9	68·8–115·0
	Sivatherium olduvaiense	128·0	126·0–130·0	74·0	65·0– 83·0
	African Sivatheriinae			73·1	64·0– 81·3
	Sivatherium giganteum	120·0			
P4	*Giraffa camelopardalis*	132·9	114·0–158·4	89·0	63·7–106·9
	Sivatherium olduvaiense	130·0	110·0–142·0	76·0	67·0– 88·0
	African Sivatheriinae			72·7	65·5– 77·3
	Sivatherium giganteum	129·0			
M1	*Giraffa camelopardalis*	103·9	88·0–119·4	78·6	67·9– 98·1
	Sivatherium olduvaiense	102·0	89·0–116·0	74·0	64·0– 81·0
	African Sivatheriinae	122·5	121·6–123·5	72·0	58·4– 89·7
	Sivatherium giganteum	107·0	100·0–115·0		
M2	*Giraffa camelopardalis*	106·8	91·6–128·0	77·8	69·7– 90·9
	Sivatherium olduvaiense	100·0		71·0	65·0– 83·0
	African Sivatheriinae	104·1	96·1–112·4	70·0	62·8– 76·0
	Sivatherium giganteum	97·0	94·0–100·0	69·0	66·0– 72·0
M3	*Giraffa camelopardalis*	107·4	91·5–122·4	61·2	47·6– 76·4
	Sivatherium olduvaiense	106·0	102·0–108·0	50·0	49·0– 51·0
	African Sivatheriinae	95·0	85·3–111·1	49·6	41·9– 60·1
	Sivatherium giganteum	93·0	92·0– 94·0	49·0	48·0– 51·0

TABLE 56. Tr. / A–P index of the different types of teeth in the extant *Giraffa camelopardalis*, and in several series of Sivatheriinae.

[1] Calculated from data from U.S.A. Museums; see Section I, chapter 5.
[2] From the African Sivatheriinae presently described.
[3] Calculated from data, according to Dietrich, 1937, 1942.
[4] From data according to Colbert, 1935.

(*b*) These observations have also been made for other Sivatheriinae on the basis of the data of Dietrich (1937, 1942) for material from Olduvai, and of Colbert (1935) for *S. giganteum* from the Siwaliks. Their results fall into the range of variation of the African Sivatherine material here described (table 56). However, the index for Dietrich's and for Colbert's M^1 fall outside the range: this peculiarity, linked with the exceptional result obtained for M^1 from the other African material, suggests that the sampling of the M^1 presently described has not been representative. Table 57 illustrates, for the various collections, the difference of their respective index from that of *G. camelopardalis*: it averages 10 units in the case of the African Sivatheriinae.

Tooth	Upper			Lower		
	Sivatherium olduvaiense[1]	African Sivatheriinae[2]	*Sivatherium giganteum*[3]	*Sivatherium olduvaiense*[1]	African Sivatheriinae[2]	*Sivatherium giganteum*[3]
DM3		−6·7			−12·5	
DM4		−7·3			−8·6	
P2	−12·9		−9·9	−9·4	−7·2	
P3	+2·9		−5·1	−17·9	−18·8	
P4	−2·9		−3·9	−13·0	−16·3	
M1	−1·9	+18·6	+3·1	−4·6	−6·6	
M_2	−6·8	−2·7	−9·8	−6·8	−7·8	−8·8
M_3	−1·4	−12·4	−14·4	−11·2	−11·6	−12·0

TABLE 57. Absolute difference between the respective Tr. / A–P index of several collections of Sivatheriinae and that of *G. camelopardalis*.

[1] Data from Dietrich, 1937, 1942.
[2] African material here described.
[3] Data from Colbert, 1935.

(*c*) The significance of the difference of means between the fossil Sivatherines and *G. camelopardalis* has been statistically tested, and has proved 'highly significant' for DM_3, P_2, P_3, P_4, M_1, M_2, M_3, M^3: 'significant' for DM_4; 'not significant' for DM^3, DM^4 and M^2.

(*d*) A further step was to estimate the Tr./A–P Index in other fossil genera and subfamilies, namely, *Palaeotragus*, *Honanotherium* and *Orasius* (data according to Bohlin, 1926). A similar low index was obtained (see table 58). Consequently it appears that the same evolutionary trend of a reduction greater for length than for breadth has been demonstrated by different phyla in the giraffid family.

Tooth	*Giraffa camelopardalis*[1]	*Palaeotragus*[2]	*Honanotherium*[2]	*Orasius*[2]	Sivatheriinae[3]
DM^2	96·68 (35)	70·84 (2)	71·91 (4)		
DM^3	86·96 (38)	78·51 (6)	80·65 (2)		80·2 (1)
DM^4	92·28 (38)	90·82 (7)	95·53 (2)		85·0 (1)
DM_2	64·44 (37)	63·14 (5)	58·82 (1)		
DM_3	66·58 (36)	66·15 (6)	61·90 (1)		54·1 (1)
DM_4	52·30 (37)	60·03 (6)	59·37 (1)		43·7 (1)
P^2	122·86 (117)	100·08 (7)	102·54 (2)	80·95 (1)	
P^3	125·12 (120)	107·73 (9)	115·41 (3)	97·95 (2)	
P^4	132·86 (116)	124·35 (9)	134·77 (4)	109·76 (3)	
M^1	103·91 (138)	108·37 (13)	106·11 (4)	101·85 (2)	122·5 (2)
M^2	106·79 (130)	105·01 (13)	109·38 (8)	97·73 (3)	104·1 (3)
M^3	107·44 (121)	101·62 (12)	108·39 (6)	91·63 (3)	95·0 (5)
P_2	87·41 (109)	83·90 (5)	77·77 (1)		70·2 (3)
P_3	91·95 (124)	84·47 (9)	77·59 (2)	70·00 (1)	73·1 (3)
P_4	89·02 (127)	82·03 (10)	82·97 (2)	77·27 (1)	72·7 (7)
M_1	78·59 (143)	82·35 (4)	74·28 (1)	65·38 (1)	72·0 (7)
M_2	77·77 (135)	79·45 (13)	87·09 (1)	69·23 (1)	70·0 (10)
M_3	61·21 (121)	50·41 (9)	55·23 (3)	52·77 (1)	49·6 (9)

TABLE 58. Transverse / A–P index in fossil and extant Giraffid teeth.
Between parentheses ( ) is the number of specimens from which the mean has been calculated.

[1] Specimens from U.S.A. Museums (see Section 1, chapter 2).
[2] Bohlin, 1926.
[3] African material here described.

Index	*Giraffa camelopardalis*[1]	*Honanotherium*[9]	*Helladotherium*[2]	*Palaeotragus*[2]	*Orasius*[2]	African Sivatheriinae[3]
Length DM^2 / Length DM^3	75·38 (36)	95·60 (1)	83·90 (3)	77·83 (3)		
Breadth DM^2 / Breadth DM^3	83·94 (36)	89·50 (1)	76·16 (3)	75·85 (6)		
Length DM^3 / Length DM^4	92·93 (38)	87·50 (1)	88·40 (4)	90·95 (8)		88·60 (1)
Breadth DM^3 / Breadth DM^4	87·47 (38)	76·60 (1)	79·54 (5)	80·00 (9)		82·90 (1)
Length P^2 / Length P^3	91·94 (122)	97·85 (2)	98·60 (2)	93·89 (10)	95·40 (1)	
Breadth P^2 / Breadth P^3	91·28 (106)	88·80 (2)	89·50 (1)	86·10 (8)	85·00 (1)	
Length P^3 / Length P^4	101·60 (121)	97·95 (2)	104·95 (2)	101·45 (10)	110·00 (1)	
Breadth P^3 / Breadth P^4	95·02 (109)	84·90 (2)	90·40 (2)	84·66 (9)	85·30 (1)	
Length M^1 / Length M^2	93·12 (127)	95·31 (6)	88·10 (2)	89·43 (13)	92·90 (1)	82·00 (11)
Breadth M^1 / Breadth M^2	91·44 (121)	94·13 (3)	86·95 (2)	92·41 (11)	96·30 (1)	97·60 (1)
Length M^2 / Length M^3	104·13 (122)	88·41 (6)	104·55 (2)	98·45 (12)	84·80 (1)	92·80 (2)
Breadth M^2 / Breadth M^3	104·12 (116)	104·18 (5)	113·01 (11)	103·71 (12)	100·00 (1)	103·20 (2)
Length P_2 / Length P_3	80·40 (109)	78·20 (1)		77·18 (6)		77·00 (2)

Breadth P_2 / Breadth P_3	76·70 (110)	77·80 (1)		75·88 (6)		67·50 (2)
Length P_3 / Length P_4	90·23 (123)	92·35 (2)		87·90 (11)	90·80 (1)	88·70 (2)
Breadth P_3 / Breadth P_4	93·17 (116)	86·20 (2)		87·47 (10)	82·20 (1)	90·00 (2)
Length M_1 / Length M_2	93·76 (135)	94·50 (1)		94·56 (5)	100·00 (1)	90·80 (4)
Breadth M_1 / Breadth M_2	94·38 (134)			98·94 (12)	94·20 (1)	98·60 (6)
Length M_2 / Length M_3	79·58 (125)	66·00 (1)		67·24 (11)	72·20 (1)	72·70 (7)
Breadth M_2 / Breadth M_3	101·34 (120)	108·00 (1)		103·37 (12)	94·70 (1)	104·20 (4)

TABLE 59. Dental Index in extant *G. camelopardalis* compared with that of several extinct giraffid groups. Between parentheses ( ) is the number of specimens from which the mean has been calculated.

[1, 2, 3] See Table 58.

Two hypotheses may be advanced to account for the relatively increased breadth of the modern teeth and the reduction in length of the total molar-premolar series relative to the length of the jaw (see Section III, chapter I, A):

(i) The maximal contact wear between contiguous teeth was observed in the fossil lower jaws, especially in M_1 and P_4, far more than in the modern jaws where it is only occasionally observed. It is also in the lower jaw that the greater length reduction has occurred: this may have been an attempt to compensate for the 'impacted' effect of the over-crowded teeth and in order to accommodate them.

(ii) The fact that the teeth decreased more in length than in breadth may be explained by the fact that there is a selective advantage in a broader grinding surface for the side-to-side masticatory movements.

Owing to the lack of a complete maxilla, one is confronted with a problem to which an answer cannot yet be supplied, namely, the disproportion between the respective length reduction in the total upper and lower dentitions.

(*e*) *Dental index:* The dental index (Section I, chapter 5) is calculated to be usually smaller in the fossil genera (*Sivatherium*, *Honanotherium*, *Helladotherium*, *Palaeotragus*, *Orasius*) for length and breadth (with constant exceptions in the dental breadth index for M^1/M^2, M_1/M_2 and M_2/M_3 (table 59). Consequently, in the dental series, a particular posterior tooth, if compared with the tooth immediately anterior to it, is relatively longer in the fossil genera than in the modern giraffe material. This indicates that the reduction in the length of individual teeth has been greater in respect of the more posterior teeth.

CHAPTER 2

DIAGNOSIS OF AFRICAN FOSSIL GIRAFFID GENERA AND SPECIES

Colbert (1935) has modified the classification of the family Giraffidae of Pilgrim (1911), Bohlin (1926) and Matthew (1929) along sound lines. Because of the limitation of the African material, it is not the purpose of this paper to criticize this classification which is generally acceptable as a basis of discussion:

Giraffidae

Large, ruminating artiodactyls, with heavy, rugose cheek teeth. The skull may or may not have horn-cores, but if they are present they show a great variety of development. Bones of cranial roof pneumatic. Lateral metapodials and digits atrophied.

Palaeotraginae

Primitive, medium-sized giraffids, having as a rule one pair of supra-orbital, frontal horn-cores. There may be a second pair of horn-cores at the anterior extremities of the frontal. Horn-cores in the form of simple tines, well developed in the males, feebly developed or absent in the females. Skull usually elongated, dolichocephalic.

Cheek teeth brachydont, with moderately coarse sculpture on the enamel. Neck and limbs slightly elongated.

Genera: *Palaeotragus* — *Achtiaria* (syn. with *Palaeotragus*).
Giraffokeryx
Okapia
Samotherium — *Alcicephalus*, *Chersonotherium*, *Shanshitherium* (syn. with *Samotherium*).
Propalaeomeryx, *Progiraffa* — Of doubtful status; placed here provisionally.

Giraffinae

Large giraffids, with a moderately brachycephalic skull. Horns variously developed, being on the parietals and frontals, and in *Giraffa* a single median horn is also present, located on the nasals. Horn-cores rounded or flattened on the ends and covered with hair. Skull roof with highly developed sinus cavities.

Cheek teeth brachydont, with heavily rugose enamel. Limbs and neck greatly elongated.

Genera: *Giraffa*
Orasius
Honanotherium

Sivatheriinae

Gigantic giraffids, with large, heavy, brachycephalic skulls. Horns variously developed, being of frontal and parietal origin. Skull roof with large sinus cavities.

Cheek teeth moderately hypsodont, with heavily rugose enamel. Limbs not elongated but very heavy. Body heavy.

Genera: *Sivatherium*. *Indratherium* (syn. with *Sivatherium*)
Bramatherium
Hydaspitherium
Helladotherium
Vishnutherium
Griquatherium
Libytherium

On the basis of the above definitions, the Hopefield giraffids which form a homogeneous group (except for one tooth, 3345, which has already been referred to *G. ?camelopardalis*, see Section II, chapter 4) may be assigned to the Sivatheriinae. Although descriptions and diagnosis of the different genera of Sivatheriinae have been published, no diagnosis (*per se*) is available in the literature for *Vishnutherium*, *Griquatherium* or *Libytherium*, yet the features of the generic types are briefly commented on. *Helladotherium* is hornless and may be excluded from consideration of the Hopefield material.

Colbert (1935) proposes the diagnoses for *Sivatherium*, *Bramatherium* and *Hydaspitherium* as follows:

Sivatherium

A gigantic Pleistocene giraffid, with four horns in the male, an anterior conical pair, arising from the frontals, and a posterior, palmate pair situated on the parietals. As in the other gigantic Siwalik giraffids there are deep pits in the temporal fossa for the temporal muscles, and on the supraoccipital for the neck muscles. The face is very short, the nasals being retracted and strongly curved. The teeth are large, with rugose enamel. Body and limbs heavy, limbs not elongated.

Bramatherium

A gigantic Upper Tertiary giraffe having four horns, two of which grow up from the fronto-parietal region, and two of which extend laterally from the parietals. Face short, with nasals considerably retracted. A large groove occupies the parietal region just below the horn-core bases as an accommodation for the temporalis muscles. Deep pits are located in the supraoccipital for the heavy neck muscles. Teeth large and heavy, with rugose enamel. Limbs and body presumably heavy and massive.

Hydaspitherium

A gigantic giraffid with two horn-cores, fused at their bases into one solid mass, on the frontal-parietal region. The face is short, the nasals retracted. There is a large parietal or temporal groove below the horn-core for the accommodation of the temporal muscles. Teeth large, quadrate, with rugose enamel. Limbs massive and not extraordinarily elongated.

From the above diagnoses it can be seen that these forms overlap considerably, except in respect of their horns. The brief descriptions, however, are not found sufficient for positive determination of the Hopefield material, and consequently various other details of the material were compared with other collections, and it became obvious that the Hopefield specimens had greatest affinity to *Sivatherium olduvaiense*, to which the homogeneous Hopefield group is assigned without hesitation.

It has already been stated (Section II, chapter I) how Hopwood (1934) first diagnosed his original Olduvai material as *Helladotherium olduvaiensis* on the basis of some teeth and a partial hind-limb. Later (Hopwood, 1936), with the discovery of 'palmated antlers', the material was referred to *Sivatherium*: Hopwood stated however that 'the antlers are not so widely palmated as in *S. giganteum*, and terminate in a recurved point'; hence, the specific determination of *S. olduvaiense*.

It is now necessary to discuss and compare the material from the various sites in Africa in regard to this diagnosis.

I. OLDUVAI AND OTHER EAST AFRICAN SITES

All the specimens from Olduvai form a homogeneous group, both from a non-metrical and metrical point of view. As a result of the fact that *Orangiatherium vanrhyni*, which was discovered and actually named earlier than *Sivatherium olduvaiense*, has now been invalidated and referred to a subspecies of *S. olduvaiense* (*vide infra*), the question of generic or specific priority does not arise any more. Consequently all the Olduvai material and the specimens related to it are assigned to *S. olduvaiense*. To this group are also referred the two specimens marked 'Marsabit Road', from Kenya.

II. LIBYTHERIUM MAURUSIUM POMEL, 1892

On the basis of a fragmented mandible containing M_3–P_4 and a part of P_3 (plate 53), Pomel proclaimed a new genus and species which he envisaged to be within the Sivatheriinae, but he does not state clearly his reasons for creating the new genus. In 1947, Arambourg assigned giraffid teeth and a scapula from Omo to *Sivatherium olduvaiense*, and in re-discussing Pomel's material, he gave as reasons for separating *Libytherium* from *Sivatherium*: (1) the premolar series is reduced; (2) P_4 has an open inner wall where paraconid and metaconid remain separated; (3) the parastylid is very developed in P_4 and in the three molars.

Furthermore, in a right mandible (1950–1–1, Muséum d'Histoire Naturelle, Paris) from Garet Ichkeul, St. Arnaud (Tunisia) (plate 52(*a*)), diagnosed as *Libytherium maurusium*, the above features are absent, and in all respects this mandible is identical to specimens at a similar stage of wear from Olduvai (Old. 6, for instance).

Arambourg (1948(*a*)) stated that excavations at St. Arnaud provided new fragments of *Libytherium*, and in particular characteristic 'antlers' ('ramures') of the Sivatheriinae. Comparison of the non-metrical and metrical features of these horn-cores (1948–1–2, 1948–1–1) (plate 51), as well as of a third (unnumbered) specimen (plate 52(*b*)) (the cast of which has been made available by the kindness of Professor C. Arambourg and Professor J. P. Lehman) with posterior horn-cores from Olduvai, Hopefield and Tierfontein, indicates a distinct similarity of all the specimens and it is considered that they must be referred to *Sivatherium olduvaiense*.

However, on the basis of Arambourg's criteria for the *Libytherium maurusium* dentition, there is no doubt that the specimen on which he based these facts is decidedly different, not only from *Sivatherium olduvaiense*, but also from specimen 1950–1–1 from Garet Ichkeul. Furthermore, these criteria are so distinctive, especially the primitive nature of P_4, that it is necessary to divide the North African material into *Libytherium maurusium* for the type specimen, and *Sivatherium olduvaiense* for the horn-cores, mandibles and other similar specimens (e.g. specimens 1948–1–1, 1948–1–2, 1949–2–937, 1949–2–938, 1949–2–725, 1931–45, 1931–8, 1931–8–110, 1950–1–90, 1950–1–1 in the Muséum d'Histoire

Naturelle, Paris) mostly as yet unpublished but examined by one of us, and to be published shortly by Professor C. Arambourg. However, it may yet become necessary to equate *Libytherium* with the rather widely varying genus *Sivatherium*.

III. GRIQUATHERIUM

Three specimens have been assigned to this genus: MMK 3685 and M $553B^1$ are described as *G. cingulatum*, and F.39 as *G. haughtoni*.

(*a*) The Makapansgat specimen M 553 B^1 has been referred to *G. cingulatum* by Cooke and Wells (1947). They state that from an examination 'it would appear that [these] lower teeth are of the correct size and form to belong to Haughton's species though probably to a smaller individual'.

From the range of variation obtained by the authors (see tables 39, 40) it is quite clear that the Makapan teeth fall within the range of the East African and the Hopefield material. In fact the breadth of M_2 of M 553 B^1 is the smallest in the range. The general form and character, which Cooke and Wells considered to be distinctive of the specimen, are identical to *Sivatherium* specimens at a similar stage of wear, e.g. Olduvai, specimen 92. Consequently, there is no basis, either metrical or non-metrical, for separating M 553 B^1 from *Sivatherium olduvaiense*; this conclusion is further confirmed by the other Sivatherine material from Makapansgat described above, which are also referred to this genus and species.

Although the lingual surface of P_3 of M 553 B is 'open' as in Pomel's P_4 (*Libytherium maurusium*, type), there is still a considerable amount of the crown hidden by the bone, the tooth having just started to erupt. Because this 'open' appearance is confined to the upper portion of the tooth, it is estimated that it would resemble Old. 6 for instance, at an equivalent stage of wear. Furthermore, the teeth are much larger than those of the Pomel specimen, and are identical to *S. olduvaiense*. The former point mentioned was the only possible doubt the authors had concerning the determination of the Makapan M 553B specimens as *S. olduvaiense*.

(*b*) MMK 3685 (*G. cingulatum* Haughton 1922): The designation of this tooth presents a number of problems. From the description of this specimen (*vide* Section II, chapter 2), the following characteristics appear to differ from those of other African specimens: (1) great breadth of the tooth; (2) relative difference in breadth of the two pillars; (3) marked cingulum forming an unusually developed proto- and hypostyle; (4) prominence of the meso- and parastyle; (5) the acute angulation of the lingual surface (in profile) to the crown-root junction; (6) the abnormal length of the posterior pillar relative to the anterior. Some, if not all, of these features may be found individually in single specimens, often in a modified form. But the above features appearing together produce this peculiarly gross form. It is certainly a Sivatherine, and it has been compared to both *Hydaspitherium* and *Sivatherium*, and it has been suggested that it is possibly even nearer *Hydaspitherium* (Bohlin, 1926; Colbert, 1935; Cooke, 1949; Singer, 1954). Nevertheless, those features in common with *Hydaspitherium* are also exaggerated and it is more massive. On this basis, and because *Hydaspitherium* has not yet been discovered in Africa, it is considered reasonable to refer this single, very worn tooth to *Sivatherium* with which it essentially shares most features.

As regards the specific designation, although it bears a resemblance to F 2993, Old. 4 and 109 from Olduvai, the latter specimens are closer to Hopefield 4027, 4023 and 4024 and share the same range of variation. MMK 3685 tends to fall just outside this group, but it is a single specimen and no other material from Africa can yet be referred to it. Furthermore there are no associated skeletal remains of the same animal. It is probable that if Cooke and Wells had all the comparative material from Olduvai and Hopefield available in 1947, they would not have referred M 533B[1] to *G. cingulatum*. It could almost be considered as a *nomen vanum*, but in the above discussion its generic nature is established. Consequently in the present state of our information it would be preferable to retain *cingulatum* as a species of *Sivatherium*.

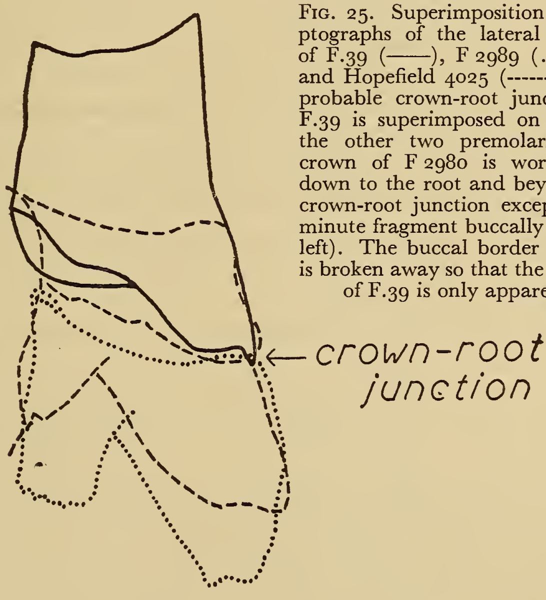

Fig. 25. Superimposition of dioptographs of the lateral aspects of F.39 (——), F 2989 (......), and Hopefield 4025 (------). The probable crown-root junction of F.39 is superimposed on that of the other two premolars. The crown of F 2980 is worn right down to the root and beyond the crown-root junction except for a minute fragment buccally (on the left). The buccal border of 4025 is broken away so that the overlap of F.39 is only apparent.

(*c*) F 39 (*G. haughtoni* Cooke 1949): In the description of the tooth (Section II, chapter 2), statistical data was presented to support the hypothesis that this specimen is not a lower molar. This may be strengthened further by comparing the specimen with known upper Sivatherine premolars, for example F 2989 and 4025 (fig. 25). It would not be difficult to reconstruct three roots on the specimen; its base fits perfectly and directly on F 2989, which is worn right down to the crown-root junction. The A–P axis and the breadth of F 39 are smaller than those of F 2989 and 4025. Comparison with other upper premolars indicates that from the points of view of other dimensions and of general appearance, F 39 may be considered as an upper premolar, probably P^3. The major objections to this diagnosis are:

(1) the extreme hypsodonty of the specimen, and

(2) the bulge on the lingual surface just below the crown-root junction.

The latter may be partly explained by the X-ray appearance (*vide supra*) and partly by individual variability. In connection with the hypsodonty, it is unfortunate that the available upper premolars of all the Sivatherine specimens are so few, and also that they are in advanced stage of wear. Consequently an adequate range of variation cannot be obtained for comparison. However, if one attempts to reconstruct available specimens such as 4025 then it would appear that the hypsodonty of F 39 may be equated. An unsatisfactory feature of this diagnosis is that the upper molar Old. 109—an almost unworn M^3—measures only 47·0 mm. Even if this difference of 20 mm. (the teeth are at approximately the same stage of wear) were decreased by a greater number of specimens widening the ranges of variations, there would still be a significant difference in height. However, it is important to consider the dentition as a whole in the skull. If one examines the fairly complete *S. giganteum* skull (15283) in B.M.N.H., it is seen that there is a distinct downward convexity in a mesio-distal direction between P^2 and M^3. Furthermore it is seen that P^4 is approximately at the summit of the convexity and consequently it is expected that P^3 and P^4 should be more hypsodont than M^3. It is thus reasonable not to exclude this specimen from *S. olduvaiense* only on the basis of its hypsodonty, particularly because it is a single specimen and the comparable series is small. However, it is felt that there are sufficient grounds to tentatively place the specimen in a subspecies, namely *haughtoni*.

Because Cooke (1949) compared this specimen with *Sivatherium* (*Griquatherium*) *cingulatum*, it is necessary to comment on his remarks. The bases of distinction drawn by Cooke for separating F.39 from *Sivatherium* (*Griquatherium*) *cingulatum* are not considered to be sufficient for a specific difference. First, the central pit of a tooth is so variable that it cannot be used for differentiating two species. Secondly, the small piece of cingulum remaining visible on the tooth indicates that the cingulum *is* marked. For these reasons, and because of the fact that these two specimens come from the same area, although the exact localities of their discovery are unknown, the probability that these two unusually gross teeth belong to the same species is not insignificant. This independent conclusion supports the view stated above that *S. cingulatum* could be considered on a subspecific level of *S. olduvaiense*. Further discoveries are required to resolve this problem.

IV. MAKAPANSGAT

It has been stated above (111 *a*) that specimens M 553 B^1 (*G. cingulatum*) and M 553 B have now been referred to *Sivatherium olduvaiense*. This also holds good for M 553 A and the other Sivatherine material described and discussed above (Section 11, chapter 3).

V. ORANGIATHERIUM

The horn-cores mentioned by van Hoepen (1932) show all typical features of those of *S. olduvaiense*, from North Africa, Olduvai and Hopefield. However, it has been mentioned that it is distinctive only for its extremely grooved appearance on its antero-medial convex surface. There are slight variations in regard to the position of the knobs, but these are known to be highly variable features.

The four teeth from the same site (C 426 A, B, C and D)—two of them showing contact surfaces, and all four presenting the same degree of wear—almost certainly belong to one individual. Lack of accurate information concerning their discovery makes it impossible to associate definitely the teeth with the horn-cores. However, it would seem likely that they belong to the same species, if not the same individual, because they are derived from a single farm. Furthermore, van Hoepen (1932) stated that the teeth most likely belong to the horns. From a morphological point of view, C 426 A, B, C and D are identical to those extreme stages of wear in the *S. olduvaiense* material, but there are some important metrical differences. C 426 A is longer and broader than the M^3 of either Hopefield or Olduvai. Although the length of the anterior and posterior pillar do not differ much from *S. olduvaiense*, the great enlargement of the metastyle in C 426 A provides it with a great increase in length. The metastyle has been noted to be a well-developed character: but it is even more prominent in this specimen than in MMK 3685.

Owing to the fragmentary nature of B, C and D, nothing can be said of the styles, but the length of the pillars, as for C 426 A, fall beyond the dimensions of the few M^3 available.

Unfortunately, the teeth are in extreme stages of wear, even the bases of the roots showing signs of attrition, and little more can be said of the distinctive features of these teeth.

Because the horn-cores are so similar to those of *S. olduvaiense* (in which some specimens have marked grooves) and because the few morphological features of the dentition are also similar to *S. olduvaiense*, the authors hesitate to provide a new species only on the basis of dental size, especially in the light of the fact that so few M^3 are available and that the growth pattern in these few teeth appears to show a marked tendency towards 'abnormalities'.

It would appear that, because of the wide range of variation within the species, gross dental metrical exaggerations should be considered on a sub-specific level until clear criteria for specific differences can possibly be elicited in specimens yet to be discovered. These dental maxima may only be ecological variations, but, on the other hand, future evidence may indicate these maxima to be of a specific nature.

Consequently, even though criteria for a 'subspecies' in fossil material are difficult to elicit and clarify, it is proposed to refer the specimens of *Orangiatherium vanrhyni* to a subspecies of *Sivatherium olduvaiense*. The question of priority which would normally arise both as regards genus and species, falls away as van Hoepen's terminology is invalidated under Article 25(*c*) of the International Code of Zoological Nomenclature. To link the specimens with discoverer, it is proposed to designate them *Sivatherium olduvaiense vanhoepeni*.

The plaster cast representative (C.1492) from Florisbad appears to fall within the range of variation of *Sivatherium olduvaiense*.

VI. ?CORNELIA, ?FLORISBAD

The two milk molars marked B_1 and B_2 are Sivatherine in form and size but nothing is recorded of the site of their discovery. Because of lack of comparative deciduous teeth and because of the fact that more than one subspecies might be represented in the Orange Free State, the authors have decided to refer these two teeth to an indeterminate subspecies of *Sivatherium olduvaiense*.

Concluding Note on Taxonomy

It is now necessary, on the basis of the above discussion, to modify Colbert's classification (1935) of the genera of the Sivatheriinae as follows:

Sivatherium syn. *Indratherium*
Bramatherium
Hydaspitherium
Helladotherium
Vishnutherium
Libytherium

As far as the African fossil Sivatherine material is concerned, the following genera, species and subspecies are recognized from 22 sites extending from North Africa to the southern tip of South Africa:

Libytherium maurusium Pomel 1892
Sivatherium olduvaiense Hopwood 1934
Sivatherium olduvaiense haughtoni
Sivatherium olduvaiense vanhoepeni, subsp. nov.
Sivatherium olduvaiense subsp. indet.
Sivatherium cingulatum

CHAPTER 3

THE FAUNAL RELATIONSHIPS AT THE AFRICAN SIVATHERINE SITES

All the available data concerning the fauna identified at the various African sites (figs. 17a, 18, 23) where Sivatherines are known to have been

Genera	Wadi Natrun	Garet Ichkeul	St. Arnaud	Omo	Kanam	Olduvai I	Olduvai II	Olduvai III	Olduvai IV	Serengeti	Olorgesailie	Makapansgat	Hopefield	Florisbad	Cornelia
**Libypithecus*	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.
**Simopithecus* incl. *Gorgopithecus*	.	.	.	.	.	x	x	x	x	.	x	x	x	.	.
Cercocebus	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.
**Cercopithecoides*	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.
**Parapapio*	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.
**Dinopithecus*	.	.	.	x	.	.	.	.	.	.	.	x	.	.	.
Choeropithecus = *Papio*	.	.	.	.	.	.	.	.	x	x	.	x	.	.	.
**Brachygnathopithecus*[1]	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.
**Australopithecus*	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.
Homo	.	.	.	.	x	.	.	.	.	.	.	.	x	x	.
Myosorex	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.
Suncus	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.
Insectiv. gen. indet.	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.
**Serengetilagus*	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.
Leporidae gen.	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.
Lepus	.	.	.	.	x	.	.	.	.	.	.	.	.	.	.
Xenohystrix	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.
Hystrix	.	.	.	.	.	x	.	.	.	x	.	x	.	.	.
Heterocephalus	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.
**Gypsorhychus*	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.
Xerus	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.
Pedetes	.	.	.	.	.	.	.	.	.	x	.	.	.	x	.
Muridae gen.	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.
Tachyoryctes	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.
Dendromus	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.
Saccostomus	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.
Colomys	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.
Canis	.	.	x	.	.	.	x	.	x	x	.	x	x	.	.
Otocyon (incl. *Prototocyon*)	.	.	.	.	.	.	.	.	x	.	.	.	.	.	.
Lycaon	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.
Vulpes	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.
Mellivora	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.
Aonyx	.	.	.	.	.	.	x	.	.	.	.	.	.	x	.

Genera	Wadi Natrum	Garet Ichkeul	St. Arnaud	Omo	Kanam	Olduvai I	Olduvai II	Olduval III	Olduvai IV	Serengeti	Olorgesailie	Makapansgat	Hopefield	Florisbad	Cornelia
Herpestes (incl. *Calogale*, *Mungos* in part) ..	.	.	.	.	.	.	.	.	.	.	.	.	x	x	.
Cynictis	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.
Atilax	.	.	.	.	.	.	.	.	.	.	.	.	.	x	.
Mungos	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.
Crocuta (incl. *Hyaena* in part)	.	.	.	.	x	x	.	.	.	x	.	x	x	.	.
Hyaena	.	.	x	.	.	.	.	.	x	x	.	x	x	x	.
Felis (incl. *Lynx*, *Leptailurus*, *Panthera*)	.	.	.	.	.	x	x	.	x	x	.	.	x	.	.
Acinonyx	.	.	.	.	.	.	x	.	.	.	.	.	.	.	.
**Machairodus*	*x*	.	.	.	.	.	.	.	.	.	.	*x*	.	.	.
**Homotherium*	.	.	.	*x*	.	.	.	.	.	.	.	.	.	.	.
Felidae gen. incl...	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.
Orycteropus	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.
**Anancus*	.	*x*	*x*	.	*x*	*x*	*x*	.	.	*x*	.	.	.	.	.
**Mammut* (=*Mastodon*)	*x*	.	*x*	.	.	.	.	.	.	.	.	.	.	.	.
Proboscid gen.	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.
**Stegolophodon*	.	.	.	.	x^2	.	.	.	.	.	.	.	.	.	.
**Stegodon*	.	.	.	.	*x*	.	.	.	.	.	.	.	.	.	.
Loxodonta (incl. *Palaeoloxodon*), } incl. *Elephas*	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.
**Mammuthus* (incl. *Archidiskodon*), } incl. *Elephas*	.	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	.	.	.	.
**Deinotherium*	.	.	.	*x*	*x*	*x*	*x*	.	.	*x*	.	.	.	.	.
Procavia	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.
**Hipparion* (incl. *Hypsohipparion*, *Stylohipparion*) ..	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	*x*	.	.	*x*
Hippotigris (=*Eurygnathohippus*, *Kolpohippus*) ..	.	.	x	x	x	x	x	x	x	x	x	x	x	x	x
Equus	.	x	x	.	.	x	x	x	x	.	.	.	.	.	.
**Chalicotherium*	.	.	.	.	.	*x*	*x*	.	.	.	.	.	.	.	.
**Metaschizotherium*	.	.	.	.	.	.	.	.	.	*x*	.	*x*	.	.	.
Ceratotherium	.	.	.	x	x	x	x	x	x	x	x	x	x	.	.
**Serengeticeros* (probably = *Ceratotherium*) ..	.	.	.	.	.	.	.	.	.	*x*	.	.	.	.	.
Diceros	.	.	.	.	x	x	x	x	x	.	.	x	x	.	.
Atelodus	.	x	x	.	.	.	.	.	.	.	.	.	.	.	.
**Sivachoerus*	*x*	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Koiropotamus (=*Potamochoerus*)	.	.	.	x	x	x	.	.	x	x	x	x	.	.	.
Sus	x	x	.	x	.	x	.	.	.	x	.	.	.	.	.

Phacochoerus (incl. *Afrochoerus*)	.	.	.	x	.	.	x	.	x	x	x	.	.	x	x
**Omochoerus*	.	.	x	x	.	.	.	.	.	.	.	.	.	.	.
Hylochoerus	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.
**Mesochoerus*	.	.	.	.	.	x	.	.	x	.	.	.	x	.	.
**Metridiochoerus* (incl. *Pronotochoerus*)	.	.	.	x	.	x	.	.	.	.	.	x	.	.	x
**Notochoerus* (incl. *Gerontochoerus*)	.	.	.	x	.	x	x	x	x	x	x	x	.	.	.
**Tapinochoerus*	.	.	.	.	.	.	.	.	.	.	.	.	x	.	x
Hippopotamus	x	x	x	x	x	x	x	x	x	.	x	x	x	x	.
Okapia	.	.	.	.	.	.	.	.	.	x	.	.	.	.	.
Giraffa	.	.	x	x	.	.	x	x	x	x	x	x	x	.	.
Camelus	x	x	.	.	.	.	.	.	.	.	.	.	.	.	.
Strepsiceros	.	.	.	x	.	.	x	.	x	x	.	x	x	.	.
Tragelaphus	.	.	.	x	.	.	.	.	.	.	.	.	.	.	.
Taurotragus	.	.	.	x	.	x	x	.	x	.	x	x	x	.	.
**Bularchus*	.	.	.	.	.	.	x	x	x	.	.	.	.	.	.
Syncerus (incl. *Bubalus* in part)	.	.	.	x	.	.	.	.	.	.	.	x	.	.	.
**Homoioceras* (incl. *Bubalus* in part)	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.
Bubalus (*Buballus*)	.	.	x	.	.	.	.	.	x	.	.	.	.	x	.
Cephalophus	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.
Philantomba	.	.	.	.	.	.	.	.	x	.	.	.	.	.	.
Kobus (incl. in part *Adenota*)	.	.	.	x	.	.	.	.	.	.	.	.	.	x	.
Adenota (incl. in part *Kobus*)	.	.	.	.	.	x	x	.	x	.	.	.	.	.	.
Redunca	.	x	.	x	.	.	.	.	x	.	.	x	x	.	.
Pelea	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.
Hippotragus	.	.	.	.	.	.	x	.	x	.	.	.	x	.	.
Oryx	.	x	x	.	.	x	x	.	x	.	.	x	.	.	.
Damaliscus	.	.	.	.	.	.	.	.	x	.	.	x	x	.	.
**Parmularius*	.	.	.	.	.	x	.	.	.	.	.	.	.	.	.
Gorgon	.	.	.	.	.	x	x	x	x	.	.	x	.	.	.
Alcephalus (=*Bubalis*)	.	x	x	x	.	.	x	.	x	.	.	x	.	x	.
**Peloroceras*	.	.	.	.	.	.	.	.	.	.	.	x	.	x	x
**Makapania*	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.
Beatragus	.	.	.	.	.	x	x	x	.	.	.	.	.	.	.
Connochaetes	.	.	.	.	.	.	.	.	.	.	.	.	x	x	.
**Lunatoceras*	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.
Oreotragus	.	.	.	.	.	.	.	.	.	.	.	x	.	.	.
Nesotragus	.	.	.	.	.	.	.	.	x	.	.	.	.	.	.
Raphicerus	.	.	.	.	.	.	.	.	.	.	.	.	x	.	.
Aepyceros	.	.	.	x	.	.	.	.	.	.	.	x	.	.	.
Gazella	.	.	.	x	.	x	x	.	x	.	.	x	.	.	x

Genera	Wadi Natrun	Garet Ichkeul	St. Arnaud	Omo	Kanam	Olduvai I	Olduvai II	Olduval III	Olduvai IV	Serengeti	Olorgesailie	Makapansgat	Hopefield	Florisbad	Cornelia
*Phenacotragus (=Adenota in part)	.	.	.	.	.	.	.	.	x	.	.	x	.	.	.
Antilope gen.	x	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Antidorcas	.	.	.	x	.	.	.	.	.	.	.	.	x	.	.
*Menelickia	.	.	.	x	.	.	.	.	.	.	.	.	.	.	.
*Pultiphagonides	.	.	.	.	.	x	x	.	.	.	.	.	.	.	.
Pelorovis	.	.	.	.	.	.	.	.	x	.	.	.	.	.	.
*Phaleroceros	.	.	.	.	.	.	.	.	x	.	.	.	.	.	.
Bos	.	x	x	.	.	.	.	.	.	.	.	.	.	.	.
	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table 60. Generic distribution of fossils identical at African Sivatherine sites (up to 1957).

* and x = extinct genus. [1] Now included in *Simopithecus* (Freedman, 1958). [2] Probably *Archidiskodon* (Singer & Hooijer, 1958).

discovered is summarized in table 60. No material from the Vaal River deposits is included in this table because the Sivatherine specimens MMK 3685 and F 39 were recovered from unknown localities, and it would be impossible to associate them with any particular faunal group from the Vaal River as the fauna are derived from series of gravels of varying geological periods, the sequences of which have not been finalized. The data concerning the O.F.S. sites is incomplete, because in the case of Tierfontein very little is known of the associated fauna, while the mass of material collected from Florisbad and Cornelia has not been identified.

It will be noted that only the genera are given in the table, because in very many cases there is dubiety about the specific identification. Furthermore, in some cases there is controversy concerning the genera themselves and some have been referred to or included in others (Hopwood and Hollyfield, 1954). Arambourg (1947) and Leakey (1958) differ, for example, as to the generic determination of the East African suidae. Purely on a statistical basis, the genera common to two or more sites have been selected and expressed in a table of correlation (table 61).

	St. Arnaud	Wadi Natrun	Olduvai I	Olduvai II	Olduvai III	Olduvai IV	Olorgesailie	Omo	Serengeti	Kanam	Makapansgat	Hopefield	Florisbad	Cornelia
Garet Ichkeul	9	4	6	7	4	7	3	6	4	4	5	3	2	1
St. Arnaud		3	7	10	6	11	5	7	7	5	7	5	5	2
Wadi Natrun			3	2	2	2	2	3	2	2	3	1	1	1
Olduvai I				20	11	17	9	12	12	10	14	9	2	4
Olduvai II					13	22	10	13	12	8	14	10	4	4
Olduvai III						12	8	7	6	6	8	5	2	2
Olduvai IV							11	14	13	7	20	14	5	4
Olorgesailie								10	8	6	8	5	3	3
Omo									11	7	14	8	4	3
Serengeti										8	12	8	4	3
Kanam											6	6	3	2
Makapansgat												12	4	3
Hopefield													6	2
Florisbad														3

TABLE 61. Genera common to two different African sites.

(See also Appendix.) Since this table was drawn up a number of extinct genera have been identified at Hopefield and at Olduvai, but they have not been included in this table.

The interpretation of such a table must be undertaken with great care because of the varying amount of material collected from different sites. This table does not express a relative time correlation. However, if one takes Olduvai, Omo, Makapansgat and Hopefield, where large numbers of specimens have been recovered and identified, the correlation becomes more representative, but the actual figures do not indicate which genera are in common to all sites. A similarity between two sites is indicated: Hopefield for example appears to have more in common with Olduvai IV than with Omo. Furthermore, if one estimates the extinct forms and the extant forms at each site, and works out the index of the relationship between extinct forms and the total, and between extinct and extant forms, one obtains an interesting gradation of series; especially if one selects arbitrarily those sites where there are more than a total of 15 recognized genera (table 62). For both indices one obtains the same gradation of increasing indices, namely, Hopefield, Olduvai IV, Serengeti, St. Arnaud, Makapansgat, Olduvai II and Olduvai I. It must be emphasized that this is not an attempt at an age sequence, but merely indicates the proportions of the extinct and extant fauna. Nevertheless there is some evidence that Hopefield overlaps the Olduvai IV period, and some of the faunal evolutionary sequences (e.g. higher crown of *Mesochoerus lategani* (Singer & Keen, 1955) compared with *Mesochoerus olduvaiensis*) and the more evolved human-manufactured stone tools (Singer & Crawford, 1958a), tend to corroborate this and even suggest that a portion of the 'Hopefield period' extends to slightly more recent times than the period indicated by Olduvai IV.

	Number of recognized genera			
	Total	*Extinct*	$\frac{\textit{Extinct}}{\textit{Total}} \times 100$	$\frac{\textit{Extinct}}{\textit{Extant}} \times 100$
Garet Ichkeul	13	3	23·1	30·0
St. Arnaud	16	4	25·0	33·3
Wadi Natrun	9	4	44·5	80·0
Olduvai I	28	10	35·7	55·6
Olduvai II	28	9	32·0	47·5
Olduvai III	13	5	38·4	62·3
Olduvai IV	35	7	20·0	25·0
Olorgesailie	11	4	36·4	57·0
Omo	26	9	34·6	53·0
Serengeti	33	8	24·3	32·1
Kanam	14	6	42·9	75·0
Makapansgat	48	15	31·2	45·5
Hopefield	30	5	16·7	20·0
Florisbad	14	1	7·1	7·7
Cornelia	7	4	57·2	132·6

Table 62

However because *all* the material from Olduvai, Makapansgat and Hopefield has not yet been definitely identified, these indices may have to be altered in time (see 'Appendix'). The data indicate clearly how, throughout Africa, a large percentage of the fossil material is extant and how these extant forms are widespread throughout the African Pleistocene. Consequently, it is not surprising that *Giraffa* has been recovered from Upper, Middle and Lower Pleistocene sites, and that *Sivatherium* has been recognized in each of the four Beds at Olduvai and even at Omo.

Confined to Stage I	Common to I–II	Confined to Stage II	Common to II–III	Confined to Stage III
Omo-Kanam		Olduvai I–II Serengeti		Olduvai III–IV Olorgesailie
Dinopithecus	*Crocuta*	*Hystrix*	*Simopithecus*	*Otocyon*
Lepus	*Anancus*	*Aonyx*	*Canis*	*Bubalus*
Syncerus	*Deinotherium*	*Acinonyx*	*Mesochoerus*	*Nesotragus*
Aepyceros	*Sus*	*Chalicotherium*	*Bularchus*	*Philantomba*
Kobus	*Metridiochoerus*	*Pultiphagonides*	*Adenota*	*Phenacotragus*
Antidorcas	*Mammuthus*	*Parmularius*	*Hippotragus*	*Redunca*
Menelickia		*Serengeticeros*	*Gorgon*	*Pelorovis*
Omochoerus		*Serengetilagus*	*Beatragus*	*Damaliscus*
Stegodon		*Heterocephalus*	*Felis*	*Thaleroceras*
Archidiskodon		*Xerus*	*Notochoerus*	
Homotherium		*Pedetes*	*Choeropithecus*	
		Tachyoryctes	*Equus*	
		Mungos		
		Orycteropus		
		Metaschizotherium		
		Hylochoerus		
		Okapia		
16·2%	8·8%	25·0%	17·6%	13·2%

Common to Stages I, II and III	
Hyaena	*Phacochoerus*
Hipparion	*Hippopotamus*
Ceratotherium	*Giraffa*
Diceros	*Alcelaphus*
Potamochoerus	*Oryx*
Gazella	*Strepsiceros*
	Taurotragus
19·2%	

Total: 68 genera.

Table 63. Correlation of East African Pleistocene Fauna.

A correlation of the East African fauna as it is presently described, according to the stages recognized (table 63), produces a number of genera (20%) common to all three stages, which is almost identical to incidences in the Hopefield material. This indicates that throughout Africa about 20 per cent of approximately 70 genera persisted (though possibly undergoing specific determination) over a great length of time, despite changing ecological and climatological conditions. Furthermore, in respect of a single genus, namely, *Giraffa*, and one single species, *camelopardalis*, which has been recovered from the Lower Pleistocene (at Omo, see Arambourg 1947), there has been no evolutionary change, despite its wide dispersal—chronological, climatological and spatial. This fact demonstrates the tremendous adaptability of *G. camelopardalis*. However, during this period, a much smaller species, *G. gracilis*, became extinct, as well as two genera (*Sivatherium* and *Libytherium*) of another subfamily (Sivatheriinae).

APPENDIX

After the MS. had been completed, three series of giraffid material were made available to the authors. Newly discovered specimens from the Limeworks breccia at Makapansgat were kindly sent by Mr. J. W. Kitching from the Bernard Price Institute for Palaeontological Research, Johannesburg. The Curator of Vertebrate Palaeontology (Dr. A. J. Sutcliffe) of the British Museum (Natural History) informed us that some more East African fossil giraffid specimens had been found in storage which had previously not been known to be available. The third series, one specimen, was discovered by one of the authors (R. S.) at Baard's Quarry, Langebaan (Cape Province), which is about 10 miles NW. of the Elandsfontein site at Hopefield. This specimen, an astragalus, had been recovered, with other bones, from the layer of phosphatic nodules about 5–10 feet below the surface. Most of the bones have been identified and they belong to animals similar to those found at Elandsfontein. Only one identifiable specimen, *Stegolophodon* sp., belongs to a much earlier horizon (Singer & Hooijer, 1958).

A. Makapansgat

Material

I. Giraffa

M 2085: Left M_2 or M_1.
M 1801: Right canine with tip of root broken off.
M 1798: Portion of left ramus of mandible with M_1 and fragmented M_2.
M 1800: Fragment of maxilla with portions of right M^1, P^4.

II. Sivatheriinae

M 2087: Fragment of mandible containing unerupted I_1, I_2.
M 2086: Fragmented right M_3.
M 539 A: Now in British Museum (Natural History) and numbered M 16729. Jaw fragment of juvenile.

Description

I. Giraffa

M 2085

This is a left lower molar, probably M_2, but the possibility of its being M_1 cannot be ruled out. It is a complete tooth with a fragment of mandible between its roots. The crown is identical in appearance to M 942—M 1113, except that

(i) M 942 has a minute ectostylid and M 2085 has no trace of it;

(ii) the stylids on the lingual surface of M 2085 are less marked than those of M 942—M 1113;

(iii) M 2085 is in a more advanced stage of wear; and

(iv) the posterior pillar of M 2085 is more rounded at the base of the buccal surface than M 942—M 1113, and M 2085 does not present the same marked indentation of the crown on the posterior surface that M 942—M 1113 has.

The roots of M 2085 are very robust, being more massive than those of the modern *G. camelopardalis*, although they are as short.

				Height	
	CROWN	Length	Breadth	*Lingual*	*Buccal*
(*a*)	Anterior pillar	15·5	25·5	19·6	16·3
	Posterior pillar	17·7	25·0	18·5	14·3
	Whole tooth	34·7	25·5		
(*b*)	ROOTS	Breadth	Height		
	Anterior ..	24·4	28·8		
	Posterior ..	23·7	28·0		

Table 64. Measurements of M 2085 (mm.).

These dimensions fall within the range of the other Makapansgat fossil *Giraffa*; the breadth falls within the range of variation (at upper end) of the modern *Giraffa camelopardalis* while the length falls just outside the range of the modern species.

This, like the other Makapansgat *Giraffa* specimens, is included in *G. camelopardalis*.

M 1801 (Pl. 23, e, f)

This is a rather worn right canine with most of the root intact. It presents no features not present in a canine of a modern *G. camelopardalis*. Its dimensions fall within the range of the modern species:

Crown:	Length:	21·5 (mm.)
	Breadth:	10·2
	Height:	18·0
Root:	Base-tip:	33+

M 1798

A portion of the left horizontal ramus of a mandible with a complete M_1 and a portion of the anterior pillar and the entoconid of M_2. The buccal portion of the mandible is partly broken away exposing the anterior root of M_1 and the sockets of the roots of P_4. The teeth are in a fairly advanced stage of wear, intermediate between the stages of M 942—M 1113 and M 2085. The general appearance of M 1798 is similar to that of the other Makapansgat fossil *Giraffa* M_2 specimens, except that it has a prominent ectostylid and only a slight hypostylid which has been worn away by the abutting anterior pillar of M_2. The anterior root of M_1 tapers towards the tip, in contrast to that of M 2085 which is rectangular.

This specimen is the only M_1 of the fossil *G. camelopardalis* in the present survey.

The remaining portion of the M_2 of M 1798 resembles the other M_2 Makapansgat specimens, being tightly wedged against the posterior pillar of M_1. On the lingual surface of the entostylid the median costa is dimpled by a V-shaped vertical depression.

(*a*) MANDIBLE: Breadth opposite M_1/M_2: *c.* 34
Height opposite P_4/M_1: *c.* 54

	M_1	Length	Breadth	Height *Lingual*	Height *Buccal*
(*b*)	Anterior pillar	15·5	23·7	*c.* 14	14·9
	Posterior pillar	16·3	23·4	*c.* 15	14·2
	Whole tooth	31·6	23·7		
	M_2				
	Anterior pillar	16·3	*c.* 23	*c.* 20	18·0
	Posterior pillar	—	—	20·6	—

TABLE 65. Dimensions of M 1798 (mm.).

M 1800

A fragment of right maxilla containing portions of P^4 and M^1. They are in a very advanced stage of wear, the most worn down of the Makapansgat *Giraffa* series.

M_1	Length	Breadth	Height *Lingual*	Height *Buccal*
Anterior pillar ..	11·5	29·0	7·0	6·5
Posterior pillar ..	—	—	—	8·2
Whole tooth ..	25+	—	—	—

Dimensions of M 1800 (mm.)

II. Sivatheriinae

M 2807

A fragment of the right body of a Sivatherine mandible, the symphyseal aspect of which fits that of M 553A perfectly (Pl. 40). A small portion of the posterior border of the body is present forming an arch with that of M 553A, but an anterior directed fracture has separated the body from the horizontal ramus about 1 cm. along the posterior border to the right of the symphysis. The anterior half of the mental foramen is present, as well as a small accessory foramen 11 mm. beyond the anterior border of the mental foramen with which it is continuous by a canal in the bone. Anteriorly the unerupted crowns of I_2 and I_3 are visible where the outer bony alveolus has been broken away and the socket for the root-tip of I_1 is visible. It is evident that I_2 is at a more advanced stage of the process of eruption than I_3 which is 'impacted' against I_2 and is partly overlapping it. The anterior enamel edge of the crown of each tooth is at an angle of about 45° to the superior surface of the body of the mandible, the medial edge of each enamel border being nearer the surface. Furthermore it is obvious that I_2 considerably overlapped the plane of I_1, indicating that during subsequent growth considerable lateral expansion of the body was still to occur so as to accommodate all the teeth (see also p.498). It is curious that there is no sign of the canine, although the broken edge of the mandible just lateral to I_3 appears to be the socket for the root. On the left this region is obscured by breccia. The order of eruption, as regards the premolar-incisor-canine teeth, then, simulates that in modern *Giraffa camelopardalis*. The enamel of the incisor is fairly rugose and the crown enamel is markedly convex, the occlusal edge of the enamel projecting vertically. If one mentally reconstructs the anterior portion of the body one obtains the conviction that the incisor would not be in the same plane as the superior surface of the body but rather at about 45° to it. This tends to confirm our opinion stated on page 498 that the incisor-canine row of the Makapansgat *Sivatherium olduvaiense* would be at an intermediate position between *Hydaspitherium* sp. (AMNH 19684) and *Giraffa camelopardalis*.

It is now possible to assess more accurately the length of the body of the mandible, namely, about 120 mm. This specimen also indicates that the height of the body of the mandible relative to the breadth of the body is greater in the immature individual. With maturation of the individual the depth decreases and the breadth increases. This principle also pertains to the modern *G. camelopardalis*.

The only measurement that can be taken on the teeth is the breadth of the crown of I_2, namely, 23·7 mm.

M 2086

This is a right M_3, broken off at the crown-root junction with the anterior pillar almost complete, the posterior pillar having the occlusal portion of the hypoconid broken off, and the talonid having most of the buccal cone broken away. The slightly rolled edge of the enamel of the occlusal surface indicates that the tip of the crown of the tooth was only just above the alveolar margin of the mandible, so that most of this specimen must still have been embedded in the mandible. This very early stage of eruption is in conformity with that at which a M_3 of M 553B^1 would have been expected to be. Furthermore, as was found with M 2087 which belongs to M 553A, it would be reasonable to conclude that M 2086 is the M_3 of the right side of the individual to which M 553B^1, M 553B, M 553 and M 2087 belong. It can also be concluded that this specimen supports the view that the order of eruption of the molars of *Sivatherium* is the same as that in *Giraffa camelopardalis*, namely, M_1–M_2–M_3 in that order.

It is interesting to note that in M 2086 the angularity of the buccal cones seen in M 553B[1] is obvious only in the second pillar of M 2086 while its anterior pillar is more rounded.

In general appearance, M 2086 closely resembles M_3 of Old. SK. II, 92, except that the parastylid of M 2086 is a more marked ridge, while the median ridge (costa) of each pillar of M 2086 is not yet as prominently developed as those of the Olduvai specimen (which is at a much later stage of eruption). The finely rugose buccal surface of M 2086 has three horizontal ridges on the enamel on the anterior pillar and one on the posterior pillar—these are more marked than in Olduvai 92.

Measurements of M 2086 (*mm.*):

	Length	Breadth	Height	
			Lingual	*Buccal*
Anterior pillar ..	28·0	33·0	49+	49+
Posterior pillar ..	22·0	29+	51+	—
Talonid	14+	19+	31+	—
Whole tooth ..	66+	33·0	—	—

It is clear that this specimen falls within the range of the measurements of *Sivatherium olduvaiense*, and, being the least worn of the M_3 series, it extends the upper range of variation of the height of the tooth to 51+ mm.

M 539A (Pl. 36, g)

This is the number given by the Bernard Price Institute for Palaeontological Research, Johannesburg, but it is now permanently in the British Museum (Natural History) where it has been given the number **M 16729**.

It is a fragment of a left mandibular ramus of a juvenile and definitely belongs to the opposite side of the Sivatherine specimen M 539B. It contains the two posterior pillars of DM4, the most anterior pillar being broken away.

Measurements of mandibular fragment (*mm.*):

Length ..	73·4
Thickness ..	31·3

B. Additional East African Specimens

The additional giraffid specimens in the British Museum (Natural History) are mainly fragmentary and are derived from Olduvai Gorge (Tanganyika), Laetolil beds (Vogel River, Tanganyika) and Broken Hill (Northern Rhodesia) (figs. 17a, 17b). Brief descriptions of the Sivatherine specimens only are given.

(*a*) Olduvai Gorge

MATERIAL

I. Giraffa

M 14778: Axis. Bed I.
M 14781: Cervical vertebra (7th). Bed I.
M 14792: Calcaneum. Bed I surface.
M 14793: Metacarpal, distal end. Bed I.
M 14794: Metatarsal, distal end. Bed I.
M 14795: Metacarpal, distal end. Bed II.
M 14796: Metatarsal, distal end. Bed II.
M 14797: Metatarsal, distal end. Bed II, surface.
M 14798: Metacarpal, proximal end. Bed I.

II. Sivatheriinae

M 14535: Horn core fragment. Bed I.
M 14779: Cervical vertebra (6th). Bed IV.
M 14780: Cervical vertebra (6th). Bed I, surface.
M 14791: Tibia. Bed III.
M 17024–6: Three molar teeth.
?: Unnumbered left lower molar. G. RK III.

III. Giraffid (no generic distinction possible)

No numbers on specimens. Letters refer to sites.

Astragalus	Oldy.	FLK	II	S	
	—	DC	II		
	—	HEK	II	S	
	—	HEK	II	S	
	—	GTS	IV	S	
	—	GRK	II	S	
Phalanx I	Oldy.	GHJK	II	S	
	—	EHK	I		
	—	DK	I	S	
	—	HEK	II		
Calcaneum ..	GRK	II	S		
Tibia	Oldy.	FC	II	S	(distal end)
	—	EK	I	S	(proximal end)
	—	SC	II	S	(proximal end)
	—	GRK	II	S	(proximal end)
	—	DK	I	base	
Cubonaviculare (Scaphocuboid)	Oldy.	THC	I	(Y)	
	—	VEK	I		
	—	SHK	II	S	

Metapodial ..	Oldy.	FC	II	S	(distal end)
	—	DK	I	S	(distal end)
	—	HEK	I		(distal end)

(*b*) Laetolil Beds

I. Sivatheriinae

M 15088: Lower molar (or premolar).
M 15089: Upper premolar.
M 15090a, b: Lower premolars.

II. Giraffid

Cubonaviculare (Scaphocuboid)	1710.5
	Lit.A.S.
Phalanx I	MnX.S.
	LIT.AS.
Astragalus	1710 S
	LIT.A.

(*c*) Broken Hill

I. Giraffa

M 12128 .. Tibia, distal end.
? .. .. Unnumbered horn-core, cervical vertebra and distal end of a femur.

II. Sivatheriinae

M 12128 .. Metacarpal, distal end. (Same number as *Giraffa* tibia.)
M 12129 .. Astragalus.

III. Giraffid

Radius, distal end.

Description of Sivatherine Specimens

M 14535

This fragment of horn core is entered in the record book as being derived from 'Middle Pleistocene Bed I Olduvai, Tanganyika, Leakey collection 1932'.

One side is slightly convex in an A–P direction and has 3 deep, wide grooves (7–8 mm. in breadth) more or less parallel to each other and to the length axis of the horn. The other surface is concave and relatively smooth.

Although it is a small fragment it is very similar to the South African specimens. It is typically Sivatherine.

M 14791

This is a complete tibia. Its dimensions are compared with the average of 5 *Giraffa camelopardalis* from Central Africa in the Musée Royal du Congo Belge in Tervuren.

		M 14791	*Giraffa camelopardalis*
Total length	.. ..	473	639
Proximal end:	Transverse	153·5	151·8
	A–P ..	138·0	92·4
Mid-shaft:	Transverse	64·3	70·6
	A–P ..	49·4	55·8
Distal end:	Transverse	101·0	109·0
	A–P ..	75·4	76·2

TABLE 66. Measurements (mm.) of M 14791 compared with *Giraffa camelopardalis.*

This again bears out the contention expressed above that *Sivatherium olduvaiense* is much shorter and has more massive extremities than the modern giraffe.

M 17024–26

These 3 teeth of *Sivatherium olduvaiense* are all derived from Bed II.

M 17024

This is a right lower molar, either M_1 or M_2. The posterior end of the posterior pillar has been broken away. It is in early wear and the enamel is very rugose. It is markedly hypsodont and the cingulum bulges slightly. The costae are very prominent, as are also the protostylid and metastylid. The roots are broken off.

Measurements (mm.) of M 17024*:*

Maximum breadth	34·6
Occlusal breadth, anterior pillar ..	17·8
posterior pillar ..	17·9
Height, lingual	42
buccal	50·4

M 17025

This right upper molar is probably M^2. The anterior pillar is partly broken away on the buccal side. The enamel is coarsely rugose. The lingual surface slopes markedly from the base in a buccal direction. The styles are very prominent. The roots are broken off.

Measurements (mm.) of M 17025*:*

Maximum length ..	49
Maximum breadth ..	43
Occlusal length ..	26·9

M 17026

This is a left M^1 or M^2 in advanced wear. There is no cingulum. There is a marked protostyle and the median costa of the anterior pillar is flattened. Most of the posterior pillar is missing and the 2 buccal roots are broken off. The lingual root forms a broad plate.

M 15088–15090

These Sivatherine teeth are from the Laetolil Beds (Vogel River) and recorded as 'Pleistocene Tanganyika. Leakey collection 1935'. M 15088 and 15090a, b are lower P_4 and M 15089 is an upper premolar.

M 15089

This right upper premolar has its crown fairly well preserved. It is finely rugose and the lingual surface has a marked slope. The median costa is very prominent. The root is broken off.

M 15090a

Its anterior root is broken away and belongs to the side opposite that of 15090b.

M 15090b

The anterior pillar is worn down and it projects much more than the posterior pillar. The enamel is very finely rugose. The buccal surface of the anterior pillar is missing and the roots are broken off.

	Length (A–P)		Breadth		Height	
	Max.	*Occlusal*	*Max.*	*Occlusal*	*Buccal*	*Lingual*
M 15088	38·7	36·2	33·0	20·0	30·6	32·5
M 15089	33·2	29·8	46·7	33·3	29·8	26·0
M 15090*a*	37·8	35·5	27·8	—	13·1	21·4
M 15090*b*	36·3	36·2	32·0	28·7	24·6	30·1

TABLE 67. Measurements (mm.).

Unnumbered GRK II Olduvai

This is a lower left molar, probably M_2. It is still embedded in matrix. The stylids are very prominent.

Measurements (mm.):

Maximum length ..	47
Maximum breadth ..	49
Occlusal breadth ..	33
Height	32

M 14778

This is an axis. The total height is 172 mm. and the total A–P length is 160 mm. The neural canal measures 40 mm. transversely and 38 mm. A–P. The inferior articular surface measures 65 mm. transversely and 77 mm. A–P.

M 14779

This is a 6th cervical vertebra. The maximum breadth of the body is 132 mm., and the inferior articular surface measures 74×57 mm.

M 14781

This is a 7th cervical vertebra from Bed I at Olduvai. The maximum breadth of the body is 115 mm., the neural canal is 45 mm. in diameter and the inferior articular surface is 104 mm. broad and 76 mm. A–P. The condyle (on superior aspect of the body) measures 67×51 mm.

M 12128 and **M 12129**

These are specimens from Broken Hill, Northern Rhodesia. It is not certain whether these are Sivatherine.

M 12128. This is a distal end of a metacarpal and measures 117×74 mm.

M 12129. This is an astragalus and measures 81×122 mm.

The following giraffid postcranial specimens are from the Olduvai Gorge. They are not numbered and no generic distinction is possible. Only relevant measurements (mm.) are given.

(i) *Astragalus*

	Max. length	A–P	Transverse
No site	106	60	70
Oldy FLK II S ..	103	61	65
,, DC II ..	101	54	63
,, HEK II S ..	111	67	73
,, HEK II S ..	102	63	65
,, GTC IV S ..	101	62	63
,, GRK II S ..	106	62	70

(ii) *Phalanx I*

	Maximum length	Shaft *A–P*	Shaft *Transv.*	Prox. end *A–P*	Prox. end *Transv.*	Distal end *A–P*	Distal end *Transv.*
Oldy GHJK II S ..	104	44	54	57	58	37	55
,, EHK I ..	121	—	—	56	59	37	53
,, DK I S ..	114	46	52	58	59	34	55
,, HEK II ..	109	44	46	54	54	37	50

(iii) *Calcaneum*

GRK II S	Maximum length	..	222
	Body: transv.	..	54
	height	..	69

(iv) *Tibia*

Distal end fragment: Oldy FC II S Transv. .. 97
A–P .. 69

Proximal end fragment (without fibular style):

		Transverse	A–P
EK I S	..	110	74
SC II S	..	105	69
GRK II S	..	87	77
DK I Base	..	87	81

(v) *Cubonaviculare* (scaphocuboid)

		Thickness	A–P	Transverse
Oldy THC I (Y)	..	42	76	103
„ VEK I	..	43	77	101
„ SHK II S	..	36	64	84

(vi) *Metapodial*

Distal end fragments:		A–P	Transverse
FC II S ..	..	50	93
DK I S ..	..	65	112
HEK I ..	..	57	105

The following giraffid postcranial specimens are from the Laetolil Beds (Vogel River, Tanganyika):

(i) *Astragalus*

		Max. length	A–P	Transverse
1710 S	..	113	58	62
LIT. A	..	102	58	62

(ii) *Phalanx I*

		Maximum	Shaft		Prox. end		Distal end	
		length	*A–P*	*Transv.*	*A–P*	*Transv.*	*A–P*	*Transv.*
MnX S	..	97	39	35	48	49	43	30
LIT. AS	..	104	57*	45	47	49	39	27

(* denotes exostosis included)

(iii) *Cubonaviculare* (scaphocuboid)

		Thickness	A–P	Transverse
1710.5	..	47	89	107
LIT. A.S.	..	40	82	105

C. Langebaan (Cape Province)

S.A.M. 11715 (Pl. 50, c, d)

This is an almost complete right astragalus (talus) now housed in the South African Museum, Cape Town. It is longer than Olduvai 102 and 107, but its general appearance is identical to theirs. It belongs to *Sivatherium olduvaiense*.

Maximum proximo-distal length	123+
Maximum A–P length medially	71
Maximum A–P length laterally	*c.* 67
Maximum breadth proximally	84+
Maximum breadth distally..	74
Maximum articular breadth proximally ..	71
Maximum articular breadth distally ..	74

Acknowledgements

A. Financial Aid

One of us (E. L. B.) received a travel grant from the United States Educational Foundation and the Fulbright Plan Organization, and a research grant from the Belgian Fonds National de la Recherche Scientifique (Brussels). The other author (R. S.) received grants from the South African Council for Scientific and Industrial Research and the Dr. C. L. Herman Research Fund, University of Cape Town. In addition, each of the authors received research grants independently from the Wenner-Gren Foundation for Anthropological Research, Inc., New York. We are exceedingly grateful to these organizations for the generosity which enabled all the fossil and recent material to be studied and collected. Furthermore, the Land Rover donated by the Wenner-Gren Foundation to the Hopefield Research Project of the University of Cape Town was extensively used for field work.

We wish to record our thanks to the Director (Dr. A. W. Crompton) and Trustees of the South African Museum, Cape Town, who have not only accepted our paper for publication in a special issue of the *Annals*, but have also subscribed a portion to its cost of publication. The major publication costs have been met by special grants: (*a*) by the South African Council for Scientific and Industrial Research and by the Council of the University of Cape Town, and (*b*) by the Belgian 'Fondation Universitaire' to the other author (E. L. B.). For this assistance we are extremely grateful.

B. Loan of Material

The following very kindly released material (including type specimens) on loan so that we could study most of the material in Cape Town: Dr. L. S. B. Leakey, Curator of the Coryndon Museum, Nairobi (to whom we are particularly grateful for his co-operation in sending all the East African fossils); Professor R. A. Dart, University of the Witwatersrand; Dr. A. S. Brink and Mr. J. W. Kitching, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand; Dr. A. C. Hoffman, Director of the Nasionale Museum, Bloemfontein; Mr. B. D. Malan, Director of the Archaeological Survey of South Africa; Mr. J. H. Power, recently Director, and Dr. R. Bigalke, present Director of the McGregor Memorial Museum, Kimberley; Professors

C. Arambourg and J. P. Lehman of the Muséum National d'Histoire Naturelle, Paris; Dr. E. Colbert of the American Museum of Natural History, New York; and Dr. A. J. Sutcliffe of the British Museum (Natural History).

C. Departments Visited, Technical Aid, Photographs

The individuals mentioned in 'B' are also thanked for giving permission to study material (mainly recent) in their Institutions. In this respect we are also grateful to Professor A. S. Romer and Dr. B. Lawrence of the Comparative Zoology Museum at Harvard University (Cambridge, Mass.); Drs. G. G. Simpson, J. Anthony and D. Carter of the American Museum of Natural History; Dr. A. W. Crompton, South African Museum, Cape Town; Dr. W. D. Turnbul of the Natural History Museum, Chicago; Dr. R. Kellogg, U.S. National Museum, Washington; Dr. E. Schouteden, Musée Royal du Congo Belge, Tervuren.

We thank Mrs. R. H. Nichols of the American Museum of Natural History for her assistance and kindness; also Mr. Kenneth Abrahams, a medical student at the University of Cape Town, who, with other students, greatly assisted on field collecting trips. Radiographs were kindly made by Drs. B. and H. Hirschon, Cape Town.

We are extremely grateful to Mr. G. McManus, Surgery Department, University of Cape Town, who patiently made most of the magnificent photographs of the specimens, and to Miss L. A. Abrahams who typed the manuscript. Mr. J. N. Darroch, Department of Mathematics, University of Cape Town, gave helpful advice with some of the statistical analyses.

Miss A. Schweizer, South African Museum, kindly assisted with the preparation of the plates.

References

Abel, O. 1904. Ueber einen Fund von *Sivatherium giganteum* bei Adrianopel. Sitzb. Kaiserl. Akad. Wiss. (Wien), Math-Naturw. Kl., *113* (1), 639–653.

Arambourg, A. 1934. Un nouveau gisement de *Libytherium*. *C.R. Ass. franç. Avanc. Sci.* (Paris), *58*, 124.

——. 1947. *Mission Scientifique de l'Omo* (1932–1933). *1*, fasc. 3, Paléontologie. Paris, Mus. d'Histoire Naturelle.

——. 1948. Un Sivathériné nord-africain: *Libytherium maurusium* Pomel. *C.R.S. Soc. Géol. France*, séance du 10 Mai 1948, 178–179.

——. 1949. Les gisement de Vertébrés villafranchiens de l'Afrique du Nord. *Bull. Soc. Géol. France*, 5 ème série, *19*, 195–203.

——. 1952. La Paléontologie des Vertébrés en Afrique du Nord française. *XIX Congrès Géologique International. Monographies régionales*. Alger 1952, 1–64.

——, & Piveteau, J. 1929. Les Vertébrés du Pontien de Salonique. *Ann. Paléont.* (Paris), *18* (2), 1–82.

Bate, D. M. A. 1951. The Mammals from Singa and Abu Hugar. In: *The Pleistocene fauna of two Blue Nile sites. Fossil Mammals of Africa*, No. 2. London: Brit. Mus. (Nat. Hist.).

Bohlin, B. 1926. Die Familie Giraffidae. *Palaeont. Sin.*, Ser. C, *4*, fasc. 1.

Brain, C. K. 1957. New evidence for the correlation of the Transvaal ape-man bearing cave deposits. *Third Pan-African Congress on Prehist., Livingstone*, 1955. London: Chatto & Windus, 143–148.

——. 1958. The Transvaal ape-man bearing cave deposits. *Transv. Mus. Mem.*, No. 11.

Brain, C. K., van Riet Lowe, C., & Dart, R. A. 1955. Kafuan stone artefacts in the post-australopithecine breccia at Makapansgat. *Nature, 175*, 16.

Broom, R. 1948. Some South African Pliocene and Pleistocene Mammals. *Ann. Transv. Mus., 21* (1), 1–38.

Colbert, E. H. 1935. Siwalik Mammals in the American Museum of Natural History. *Trans. Amer. Phil. Soc.*, N.S. *26*, 401.

Cooke, H. B. S. 1949. Fossil Mammals of the Vaal River deposits. Dept. of Mines, *Geol. Survey of the Union of S. Afr.*, Mem. No. 35 (pt. 3).

——, & Wells, L. H. 1947. Fossil Mammals from the Makapan Valley, Potgietersrust. III. Giraffidae. *S. Afr. J. Sci., 43*, 232–235.

Dart, R. A. 1954. The significance of Makapansgat. *Z. Morph. Anthrop., 46* (2), 119–123.

——. 1957. The osteodontokeratic culture of *Australopithecus prometheus*. *Transv. Mus. Mem.*, No. 10.

Dietrich, W. O. 1937. Die Pleistozäne Giraffiden und Bovinen aus Oldoway, Deutsch-OstAfrika. In: *Wissenschaft. Ergebnisse der Oldoway Exped.* 1913, Dr. H. Reck edit.

——. 1942. Altestquartäre Säugetiere aus der südlichen Serengeti, Deutsch-OstAfrika. *Palaeontographica, 94*, A, 43–133.

Drennan, M. R. 1954. Saldanha Man and his Associations. *Amer. Anthropologist, 56*, 879–884.

Dreyer, T. F. 1938. The Archaeology of the Florisbad deposits. *Arg. Nav. Nasion. Mus.*, Bloemfontein. Pt. 1 (8), 65–77.

——, & Lyle, A. 1931. *New Fossil Mammals and Man from South Africa*. Dept. Zool., Grey Univ. Coll., Bloemfontein, 60 pp.

Ewer, R. F., & Singer, R. 1956. Fossil Carnivora from Hopefield. *Ann. S. Afr. Mus., 42* (pt. 4), 335–347.

Falconer, H. 1868. Palaeontological Memoirs and Notes. Vol. I, *Fauna Antiqua Sivalensis*. Edit. Ch. Murchison. London, Hardwicke.

——, & Cautley, P. T. 1836. *Sivatherium giganteum*. A new fossil ruminant genus, from the valley of Markanda, in the Siwalik branch of the Subhimalayan Mountains. *Asiatic Res., 19* (pt. 1).

—— ——. 1846–49. Fauna antiqua sivalensis (Plates). (Description of the plates: 1868, in *Palaeont. Mem., 1*). London.

Freedman, L. 1957. The Fossil Cercopithecoidea of South Africa. *Ann. Transv. Mus., 23* (pt. 2), 121–262.

Gaudry, A. 1861. Note sur la Giraffe et l'*Helladotherium* trouvés à Pikermi (Grèce). *Bull. Soc. Géol. France*, (2) *18*, 587.

——. 1867. *Animaux fossiles et Géologie de l'Attique*. Paris, 2.

——. 1873. *Animaux vertébrés fossiles du Mont Léberon* (Vaucluse). Paris.

Haughton, S. H. 1922. A note on some fossils from the Vaal River Gravels. *Trans. Geol. Soc. S. Afr., 24*, 11–16. (The volume relates to 1921, but was published in 1922.)

Hooijer, D. A., and Singer, R. 1960. Fossil Rhinoceroses from Hopefield. *Zool. Mededelingen Rijksmus. Nat. Hist.*, Leiden. (In the press.)

Hopwood, A. T. 1934. New fossil mammals from Olduvai (Tanganyika Territory). *Ann. & Mag. Nat. Hist.* (10) *14*, 546–550.

——. 1936. New and little-known fossil mammals from the Pleistocene of Kenya Colony and Tanganyika Territory. *Ann. & Mag. Nat. Hist.* (10) *17*, 636–641.

——, & Hollyfield, J. P. 1954. An annotated bibliography of the fossil Mammals of Africa (1742–1950). *Fossil Mammals of Africa*, No. 8. London: Brit. Mus. (Nat. Hist.).

Howell, F. C. 1955. The age of the Australopithecines of Southern Africa. *Amer. J. Phys. Anthrop., 13* (4), 635–662.

Khomenko, I. 1913. La faune méotique du village Taraklia district de Bendery. *Ann. Géol. et Minér. de la Russie.* 15, livraison 4–6.

Kormos, T. 1911. Der Pliozäne Knochenfund bei Polgardi. *Földtani Közlöni* (Budapest), *41* (1–2).

Lankaster, E. R. 1907. The origin of the lateral horns of the giraffe in foetal life on the area of the parietal bones. *Proc. Zool. Soc.*, London, *1*, 100–115.

Leakey, L. S. B. 1951. *Olduvai Gorge*. Cambridge Univ. Press.

——. 1958. Some East African Pleistocene Suidae. *Fossil Mammals of Africa*, No. 14. London, Brit. Mus. (Nat. Hist.).

Lydekker, R. 1904. On the subspecies of *Giraffa camelopardalis*. *Proc. Zool. Soc.* London, 1, 202–227.

——. 1913. Catalogue of ungulate mammals in the British Museum (Nat. Hist.). Vol. I, *Artiodactyla, family Bovidae*. London, p. 249.

Mabbutt, J. A. 1956. The physiography and surface geology of the Hopefield fossil site. *Trans. Roy. Soc. S. Afr.*, *35* (1), 21–58.

Matthew, W. D. 1929. Critical observations upon Siwalik Mammals. *Bull. Amer. Mus. Nat. Hist.*, *56*, 437–560.

Mecquenem, R. de. 1924. Contribution à l'étude des fossiles de Maragha. *Ann. Paléont.* (Paris), *23*, 135–160.

Meiring, A. J. D. 1956. The macrolithic culture of Florisbad. *Res. Nas. Mus.* (Bloemfontein), *1* (9), 205–230.

Oakley, K. P. 1954*a*. Study tour of early hominid sites in Southern Africa, 1953. *S. Afr. Archaeol. Bull.*, *9* (35), 75–87.

——. 1954*b*. The dating of the Australopithecinae of Africa. *Amer. J. Phys. Anthrop.*, *12* (1), 9–28.

Osborn, H. F. 1892. Nomenclature of mammalian molar cusps. *Amer. Natur.*, *26*, 436–437.

——. 1907. *Evolution of mammalian molar teeth to and from the triangular type*. New York, Macmillan.

Owen, R. 1840–45. *Odontography, or a Treatise on the comparative anatomy of the teeth*. London, Bailliere.

——. 1849. Notes on the birth of the Giraffe at the Zoological Society's Gardens, and description of the foetal membranes and of some of the natural and morbid appearances observed in the dissection of the young animal. *Trans. Zool. Soc.*, *3*, 21–28.

Pethö, J. 1885. Über die fossilen Säugethier-Überreste von Baltavar. *Jahresb. K.U. Geol. Anst. f.* 1884 (Budapest).

Pilgrim, G. E. 1911. The fossil Giraffidae of India. *Palaeont. Ind.*, N.S. *4* (1), 1–29.

Pomel, A. 1892. Sur le *Libytherium maurusium*, grand ruminant du terrain pliocène plaisancier de l'Algérie. *C.R. Acad. Sci.* (Paris), *115*, 100–102.

Reygasse, M. 1921. Etudes de Palethnologie maghrebine (nouv. série). *Rec. Not. Mém. Soc. Archéol. Constantine*, 5 sér., *9* (52) (1919–20), 513–570.

Roman, F., & Solignac, M. 1934. Découverte d'un gisement de Mammifères pontiens à Douaria (Tunisie septentrionale). *C.R. Acad. Sci.* (Paris), *199*, 1649–1650.

Schlosser, M. 1921. Die Hipparionenfauna von Veles in Mazedonien. *Abhdl. Bayer. Akad. Wissen*, *29*, 4.

Singer, R. 1954. The Saldanha skull from Hopefield, South Africa. *Amer. J. Phys. Anthrop.*, n.s. *12* (3), 345–362.

——. 1956. Man and Mammals in South Africa. *J. Palaeont. Soc. India*, *1*, 122–130.

——, & Keen, E. N. 1955. Fossil Suiformes from Hopefield. *Ann. S. Afr. Mus.*, *42* (pt. 3), 169–179.

——, & Crawford, J. R. 1958*a*. The Significance of the Archaeological Discoveries at Hopefield. *J. Roy. Anthrop. Inst.*, *88* (pt. 1), 11–19.

——, & Hooijer, D. A. 1958*b*. A Stegolophodon from South Africa. *Nature*, *182*, 101–102.

Stromer, E. 1907. Fossile Wirbeltier-Reste aus dem Uadi Fâregh und Uadi Natrûm in Äegypten. *Abh. Senckenb. naturf. Ges.* (Frankfurt a.M.) *29* (2), 99–132.

Van Hoepen, E. C. N. 1932. Voorlopige beskrywing van Vrystaatse Soogdiere. *Paleont. Nav. Nas. Mus.*, Bloemfontein, Dl. 2, 63–65.

Wells, L. H., & Cooke, H. B. S. 1957. Fossil Bovidae from the Limeworks Quarry, Makapansgat, Potgietersrus. *Palaeont. Afric.*, *4*, 1–55. (The volume relates to 1956 but was published in 1957.)